Acta Botanica Hungarica

VOLUME 35, NUMBERS 1–4, 1989

Akadémiai Kiadó, Budapest

ACTA BOT. HUNG. 35(1–4) 1–332 (1989) HU ISSN 0236-6495

ACTA BOTANICA

A QUARTERLY OF THE HUNGARIAN ACADEMY OF SCIENCES

Acta Botanica publishes original reports on botanical subjects in English, French, German, Spanish and Russian

Acta Botanica is published in yearly volumes of four issues by

AKADÉMIAI KIADÓ
Publishing House of the Hungarian Academy of Sciences
H-1117 Budapest, Prielle Kornélia u. 19—35.

Manuscripts and editorial correspondence should be addressed to
Acta Botanica 1363 Budapest P.O. Box 24

Subscription information

Orders should be addressed to

KULTURA Foreign Trading Company
1389 Budapest P.O. Box 149

or to its representatives abroad

Acta Botanica Hungarica is abstracted/indexed in Biological Abstracts, Chemical Abstracts, Current Contents–Agriculture, Biology and Environmental Sciences, Excerpta Botanica, Excerpta Medica

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ACTA BOTANICA HUNGARICA 35/1-4

1989

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PRINTED IN HUNGARY

Akadémiai Kiadó és Nyomda Vállalat, Budapest

Acta Botanica Hungarica 35(1-4), pp. 3-38 (1989)

EINFLUSS ERHÖHTER UV-B STRAHLUNG ALS FOLGE DES OZONABBAUES DER STRATOSPHÄRE AUF DEN STICKSTOFF-METABOLISMUS VON MIKROORGANISMEN

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A depletion of stratospheric ozone layer may lead to an enhanced level of ambient solar UV radiation on the earth's surface. In laboratory and field experiments we studied the impact of UV-B on pigmentation, protein and lipid contents as well as on the carbon and nitrogen metabolisms of microalgae and phytoplankton. A species-dependent response to UV-B stress was found which may result in a variation of the community composition of the marine ecosystem and can affect the nutrient chain. Assimilation of nitrogenous compounds was more sensitive to UV-B radiation than the carbon metabolism. In all tested microorganisms changes in the pattern of amino acids and amides was found after UV-B exposure. The results were discussed with reference to the possible targets of UV-B radiation and the damages in the supply with ATP and carbon skeletons for amino acid and protein biosynthesis.

Einleitung

Im Laufe der Erdgeschichte entstand die derzeit vorhandene Ozonschicht der Stratosphäre insbesondere durch die O_2-Entwicklung der photosynthetisch aktiven Organismen. Dabei spielten die Cyanobakterien, die der damals vorhandenen UV-Strahlung ausgesetzt waren, eine wichtige Rolle. Die frühen prokaryontischen Organismen mussten in der Lage sein, die schädigende Wirkung des UV, z. B. auf Nukleinsäuren, Proteine und Photosyntheseapparat, durch entsprechende Reparaturmechanismen aufzuheben. Andererseits könnte ein UV-absorbierendes Pigment die Zelle vor dem schädigenden Einfluss der UV-Strahlen geschützt haben. Mit der Zunahme der stratosphärischen Ozonschicht gelangte die kurzwellige UV-Strahlung nicht mehr auf die Erdoberfläche, und die Intensität der UV-Strahlung nahm ab. Parallel dazu verlief die Entwicklung von den Prokaryonten zu den heutigen höheren Pflanzen. Diese phylogenetischen Entwicklungstrends entsprechend der Ab-

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Vortrag am 8. Oktober 1987 im Gebäude der Akademie der Wissenschaften in Budapest.

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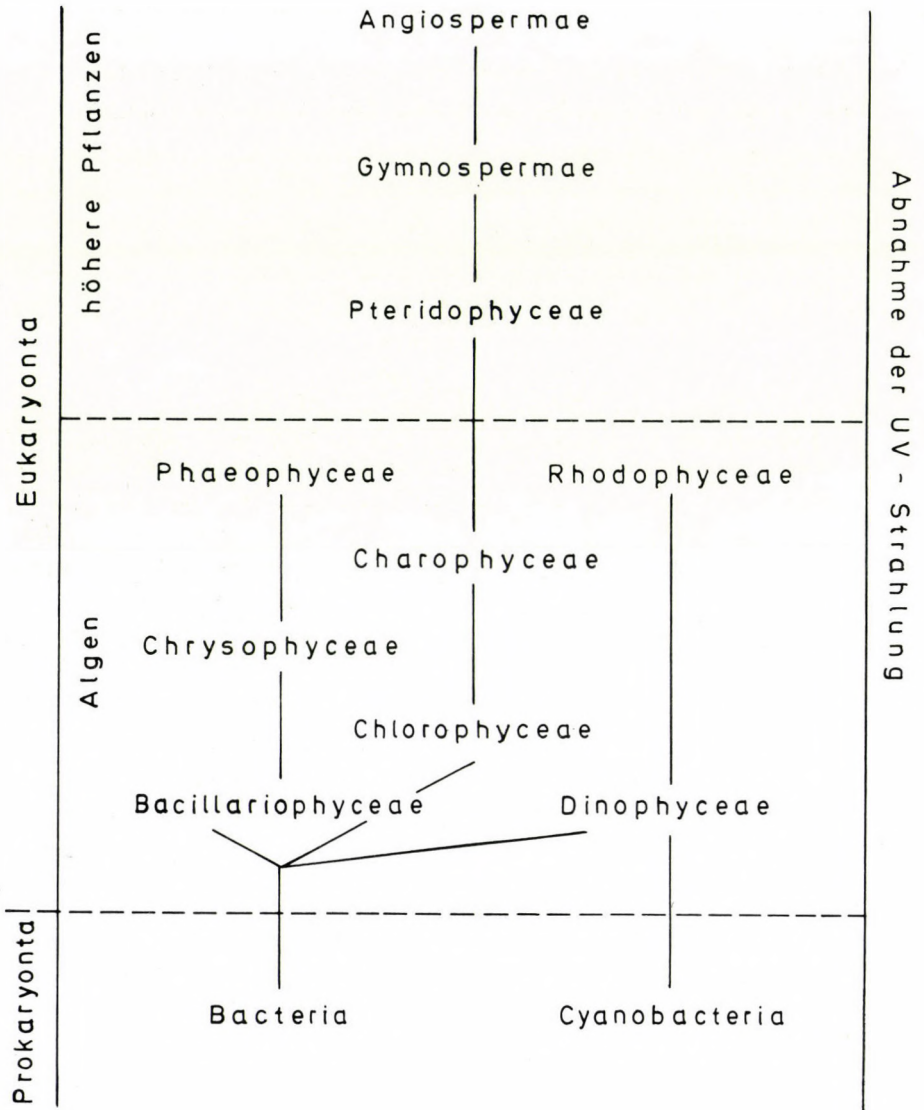


Abb. 1. Vereinfachtes Schema der phylogenetischen Entwicklung von Prokaryonten zu den höheren Pflanzen in Verbindung mit der Reduktion der auf die Erdoberfläche treffenden UV-Strahlung

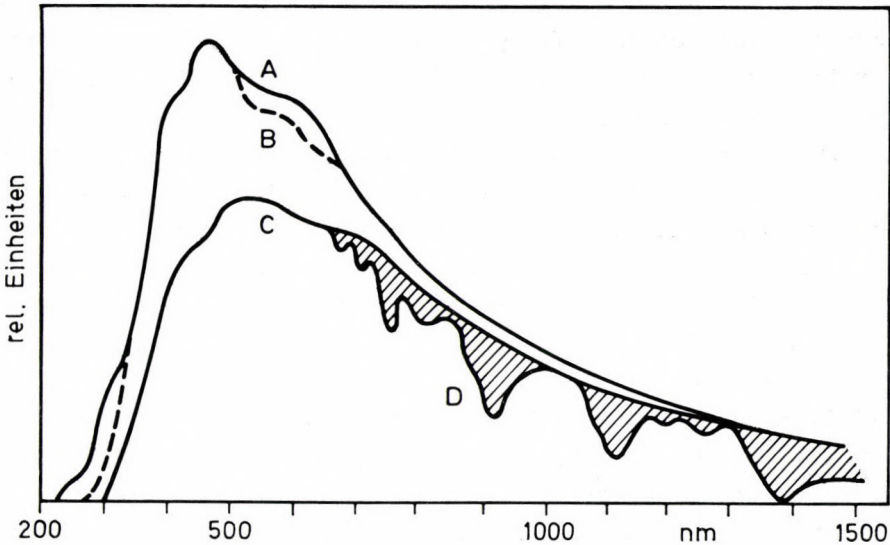



Abb. 2. Veränderungen des Absorptionsspektrums des Sonnenlichts beim Eintritt in die Atmosphäre. A: extraterrestrisches Sonnenlicht, B: nach Absorption durch die Ozonschicht, C: nach Aerosol-Streuung und D: das auf die Erdoberfläche treffende Licht nach weiterer Absorption

nahme der UV-Strahlung sind in einem vereinfachten Schema der Abb. 1 dargestellt. YENTSCH und YENTSCH (1982) haben die Absorptionsspektren mehrerer Cyanobakterien und Algen untersucht und diese in Beziehung zu einem UV-schützenden Pigment sowie zur phylogenetischen Entwicklung gesetzt. So weist das Spektrum von Oscillatoria erythrea im Bereich von 350- 450 nm eine weitaus höhere Absorption auf als das von Phaeodactylum tricornutum. Die Absorptionsspektren des stickstoffixierenden Cyanobakteriums Anabaena cylindrica weisen nach UV-B-Strahlung entsprechend der Dosis erhöhte Absorption bei 320 nm auf, was als UV-schützende Reaktion interpretiert werden kann (DÖHLER, BTP-Bericht 2/87).

Die spektrale Energieverteilung der Sonnenstrahlung verändert sich beim Durchtritt durch die Atmosphäre in verschiedener Weise (vgl. Abb. 2). Die Kurve A zeigt das Spektrum des extraterrestrischen Sonnenlichts. Nach Absoprtion durch die Ozonschicht kommt es zu einer Verlagerung zum längerwelligen Bereich des Spektrums und Verminderung der Strahlungsintensität im UV (Kurve B). In Folge von Streueffekten treten Veränderungen vor allem im Infrarot auf (Kurve C). Das letztlich auf die Erdoberfläche treffende Sonnenlicht zeigt die Kurve D der Abb. 2. Eine weitere Veräderung der spektralen Zusammensetzung des Lichts tritt beim Eintritt in die Wassersäule

auf. Neben der Reflektion an der Wasseroberfläche erfolgt eine weitere durch im Wasser vorhandene Partikel. Je nach Wassertiefe werden die Wellenlängenbereiche von Rot (in geringen Wassertiefen) nach Violett, je nach Wassertyp, total absorbiert. In klaren ozeanischen Gewässern dringen der UV- und Blau-Anteil des Sonnenlichts in 100 bzw. 200 m Tiefe ein. In Seen und Flüssen wird bereits in geringen Tiefen in Folge der Verunreinigungen und vorhandenen Huminstoffe der grösste Teil des Sonnenlichts absorbiert.

Die weltweite Nettoprimärproduktion der Pflanzen wird auf ca. 172,5 x 10^9 t Trockengewicht pro Jahr geschätzt; davon entfallen 55,0 x 10^9t auf das marine Phytoplankton (WHITTAKER und LIKENS, 1975). Die Diatomeen - der Hauptbestandteil des Phytoplanktons - sind mit 20-30% an der gesamten Primärproduktion der Erde beteiligt und weisen eine im Vergleich zu den Landpflanzen höhere Leistungsfähigkeit auf. Dies dokumentiert die Bedeutung des Phytoplanktons als Primärproduzent für die Nahrungskette im aquatischen Ökosystem. Eine Veränderung des Gleichgewichts durch menschliche Eingriffe z. B. Umweltchemikalien, die zum Abbau der Ozonschicht führen, hat auch negative Auswirkungen auf die Artenzusammensetzung und die Nahrungskette.

In der Nährstoffversorgung des marinen Phytoplanktons ist der Stickstoff oft ein limitierenden Faktor. Die Stickstoffquellen des Meeres sind NH_4^+(0,1 - 5 μM), NO_3^-(0,01 - 50 μm), NO_2^-(0,01 - 5 μM) und Harnstoff (0,1 - 5 μM). In Küstennähe und Flussmündungen sind vor allem Nitrit und Ammonium anzutreffen. Der Kohlenstoff- und Stickstoffmetabolismus sind für die Pflanze lebenswichtige Prozesse, sie stehen in Wechselbeziehung miteinander (vlg. Abb. 3) und konkurrieren um die von der Lichtreaktion der Photosynthese bereitgestellte Energie (ATP und $NADPH_2$). Nach dem Transport des Nitrats in das Zellinnere wird dieses in der Regel im Cytoplasma zu Nitrit reduziert und in die Chloroplasten transportiert, wo die weitere Reduktion zu NH_3 erfolgt. Dort wird die Aminogruppe auf Glutamat übertragen und unter Beteiligung der Glutaminsynthetase Glutamin gebildet. Die Glutamatsynthase überträgt eine Aminogruppe auf die α-Ketoglutarsäure wobei 2 Moleküle Glutamat entstehen. Aus Intermediaten der photosynthetischen CO_2-Fixierung (Calvin-Cyclus) können weitere α-Ketosäuren zur Aminosäurebiosynthese bereitgestellt werden (vgl. Abb. 3).

Neuerdings steht die Diskussion über den Ozonabbau in der Stratosphäre vor allem durch das beobachtete "Ozonloch" über der Antarktis im Vordergrund. So war im Oktober 1986 über der Antarktis in einem Bereich von ca. 10 Mio. km^2 das Ozon völlig verschwunden. Im Gebiet 35^o südlicher Breite betrug die Ozonreduktion noch 10%. Als Ursache für den Ozonabbau

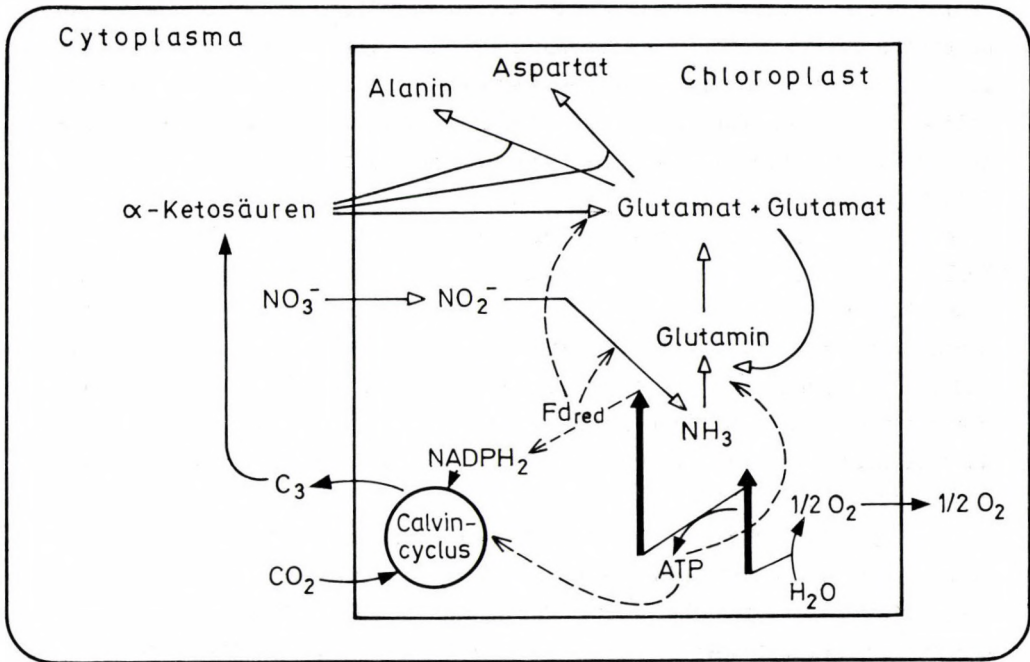



Abb. 3. Beziehung zwischen der Lichtreaktion der Photosynthese und der CO_2-Fixierung zum Stickstoffmetabolismus der Zelle. Weitere Angaben siehe Text

$$NO + O_3 \longrightarrow NO_2 + O_2$$

$$NO_2 + O \longrightarrow NO + O_2$$

$$O_3 + O \longrightarrow O_2 + O_2$$

$$Cl + O_3 \longrightarrow ClO + O_2$$

$$ClO + O \longrightarrow Cl + O_2$$

$$O_3 + O \longrightarrow O_2 + O_2$$

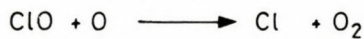



Abb. 4. Vereinfachte Reaktionsgleichungen über den Ozonabbau durch Stickoxide und Fluorchlorkohlenwasserstoffe

kommen anthropogene Einflüsse (Stickoxide, Fluorchlorkohlenwasserstoffe) in Betracht. Die vereinfachten Reaktionsgleichungen der Abb. 4 veranschaulichen den Ozonabbau durch die oben genannten Verbindungen. Nach den derzeitigen Modellberechnungen der Meteorologen soll der Ozonabbau etwa 5% betragen. Dies würde zu einer Verlagerung zum kürzerwelligen Bereich des Sonnenspektrums und Erhöhung der Intensität des UV-Anteils führen. Als Folge dessen treten Schäden in den biologischen Systemen auf: Reduktion der Zellinhaltsstoffe und des Zellstoffwechsels sowie Veränderungen im Artengefüge. Die erhöhte UV-B-Strahlung verursacht eine Verminderung der Biomasseproduktion mit entsprechend negativen Auswirkungen auf die Nahrungskette und die Fixierung des im Meer gelösten CO_2. Letzteres könnte zu einer Beeinträchtigung des CO_2-Austausches zwischen Atmosphäre und Meer führen. Es wäre denkbar, dass dies zu einer Verstärkung des Treibhauseffektes beitragen würde (vgl. Abb. 23).

Seit den Arbeiten von STEEMANN NIELSEN (1964) liegen mehrere Untersuchungen über den Einfluss des UV-Anteils des Sonnenlichts auf die Primärproduktion des Phytoplanktons vor. Durch Ausfiltern der UV-Strahlung konnte gezeigt werden, dass die Biomasseproduktion des marinen Phytoplanktons nahe der Wasseroberfläche durch den natürlichen UV-Anteil der Sonnenstrahlung um bis zu 30% reduziert wird (LORENZEN, 1979; SMITH et al., 1980). Ebenfalls wurde eine unterschiedliche UV-Resistenz der einzelnen Arten des Phytoplanktons gefunden (WORREST et al., 1978).

So beobachteten CALKINS und THORDARDOTTIR (1980), dass die Sonnenstrahlung eines normalen Sommertages für viele Diatomeenarten tödlich war und die Zahl der Cyanobakterien anstieg. Die Auswirkungen der UV-B-Strahlung auf das Phytoplankton, insbesondere die Pigmentierung und die Photosynthese, sind von mehreren Forschergruppen bearbeitet worden (HALLDAL, 1979). In dem vorliegenden Beitrag wird der Einfluss der UV-B-Strahlung vor allem auf die Zellinhaltsstoffe und den Stickstoffmetabolismus von Meeresdiatomeen und Phytoplankton näher eingegangen.

Material und Methoden

Für die Untersuchungen der UV-B-Wirkung sind einerseits Reinkulturen von Mikroalgen, vor allem Meeresdiatomeen und andererseits natürliche Phytoplanktonpopulationen verwendet wordent. Stammkulturen und Isolate von marinen Diatomeen wurden uns von Herrn Prof. Dr. A. VON STOSCH, Dr. E. HAGMEIER, Dr. M. ELBRÄCHTER und Dr. JAHNKE zur Verfügung gestellt. Die Grünalge *Chlorella fusca* (Stamm 211-8b), die Rotalge *Porphyridium purpureum* (Stamm 1380-1a) und Cyanobakterien *Anabaena cylindrica* (Stamm 1403-2) und *Synechococcus leopoliensis* (Stamm 1402-1)

wurden von der Algenreinkulturensammlung, Göttingen bezogen. Die Diatomeenarten Bellerochea Yucatanensis v. Stosch, Ditylum brightwellii (West) Grunow, Lauderia annulata Cleve, Lithodesmium variabile Takano, Odontella sinensis Greville, Synedra planctonica v. Stosch und Thalassiosira rotula Meunier sind unter folgenden Anzuchtsbedingungen kultiviert worden: Nährlösung nach v. STOSCH und DREBES (1964), Salzkonzentration 35‰, normale atmosphärische Luft (0,035 Vol.% CO_2), Licht/Dunkel-Wechsel von 14 : 10 bzw. 12 : 12 und 16 : 8 h, bei +18 °C und einer Lichtintensität von 8 W m^{-2} (etwa 3000 Lux). Die Anzuchtstemperaturen waren für Chlorella 30 °C, Porphyridium 20 °C, Anabaena 23 °C und Synechococcus 32 °C. Als Nährlösungen wurden benutzt: Für Chlorella nach DÖHLER (1972), Porphyridium nach PINTNER und PROVASOLI (1968), Synechococcus nach DÖHLER und KOCH (1972) und Anabaena nach ALLEN und ARNON (1955).

Die natürlichen Planktonproben sind vor Helgoland entnommen und in verschiedenen Wassertiefen und in UV-transparenten und UV-undurchlässigen Plexiglasgefässen erneut exponiert worden. Der Hauptanteil der autotrophen Zellen bestand aus Phaeocystis pouchettii sowie Rhizosolenia setigera, Chaetoceros spec., Ceratium fusus und Dinophysis acuminata.

Zur Bestrahlung der Algenreinkulturen wurden UV-Röhren der Fa. Philips (TL 40/12, TL 20/12) und cut-off-Filter (WG 305 der Fa. Schott u. Gen., Mainz; Dicke 3 mm) benutzt. Die verschiedenen UV-B-Intensitäten sind durch unterschiedliche Entfernungen zur Bestrahlungsquelle und verschiedene Bestrahlungszeiten erzielt worden. Als Wichtungsfunktion für die UV-B-Effekte wurde die von CALDWELL (1971) gewählte. Fürd die Bestrahlung mit Weisslicht fanden Leuchtstoffrühren (Osram L 36 W/11) und mit monochromatischem Licht eine Xenon-Hochrducklampe (2500 W) sowie Interferenzfilter der Fa. Balzers, Liechtenstein (454, 544, 604, 624, 670 nm; 436 mW m^{-2}) Verwendung. Für diese Bestrahlungsexperimente mit UV-B wurden temperierbare Quarzkulturröhren bzw. UV-durchlässige Gefässe oder Assimilationskammern mit einer Quarzscheibe benutzt. Die Freilandexperimente sind mit speziellen UV-transparenten und UV-durchlässigen Plexiglasgefässen durchgeführt worden. Die Lichtintensität wurde mit einem Messgerät der Fa. International Light bzw. Optronic Lab. Inc., USA gemessen.

Chlorophyll a und c_1+c_2 der Diatomeen wurde nach JEFFREY und HUMPHREY (1975) und Chlorophyll a und Phycocyanin der Grün- und Rotalgen bzw. der Cyanobakterien nahc JONES und MYERS (1965) bestimmt. Der Proteingehalt ist nach BRADFORD (1976) erfasst worden. Die Trennung und Analyse der Aminosäuren und Amide erfogte mittels HPLC nach der bei DÖHLER und ZINK (1984) beschriebenen Methode. Den während der exponentiellen Wachstumsphase geernteten Mikroalgen und Planktonproben sind $^{15}NH_4Cl$ (96 Atom%), ^{15}N-Harnstoff (96 Atom%) oder $K^{15}NO_3$ (96,8 Atom%) verschiedener Konzentrationen appliziert worden. Entsprechend der Fragestellung sind die Proben zu verschiedenen Zeiten und unterschiedlichen Versuchsbedingungen entnommen worden. Zur Bestimmung der Aufnahmeraten sind die Algen auf Whatman-Filter (GF/C) gesaugt und zur Erfassung des ^{15}N-Einbaues in die Aminosäuren bzw. Proteine in 80%igem Ethanol extrahiert worden. Die weitere Probenaufbereitung erfolgte nach der Dumas-Methode (FAUST, 1967) und die Messung der ^{15}N-Anreicherung mit einem Emissionsspektrometer Statron NOI 5 der Fa. Zeiss, Jena. Die ^{15}N-Analysen sind nach der Prozedur von DÖHLER und ROSSLENBROICH (1981) und die ^{14}C-Untersuchungen nach DÖHLER (1972) durchgeführt worden. Die Möglichkeiten der Anwendung der ^{15}N-Tracer-Technik zeigt die Zusammenstellung der Abb. 5. Der Kohlenstoff- und Stickstoffgehalt wurden mit dem Analysator der Fa. Carlo ERba, Modell 1106 ermittelt.

Im optischen Test sind folgende Enzymaktivitäten bestimmt worden: Aspartat- (E.C. 2.6.1.1) und Alanin-Aminotransferase (E.C. 2.6.1.2) nach HATCH und MAU (1972); Glutaminsynthetase (E.C. 6.3.1.2) und Glutamatsynthase (E.C. 1.4.1.14) nach SHAPIRO und STADTMAN (1970) bzw: GROAT und VANCE (1981).

	Transformation[a]	Isotope
Stickstoff-Assimilation		
anorganische N-Verbindungen	$(NO_3^-, NO_2^-, NH_4^+) \rightarrow$ PON	^{15}N, ^{13}N, ^{35}CI (^{14}C, ^{35}S)[b]
organische N-Verbindungen	(Harnstoff, Amino-N) $\rightarrow$ PON	^{15}N, ^{14}C, ^{3}H
N_2-Fixierung	$N_2 \rightarrow$ PON	^{15}N
Stickstoff-Remineralisierung		
Abbau organischer N-Verbindungen	PON $\rightarrow$ DON	^{15}N, ^{14}C, ^{125}I
Ammonifikation	(PON, DON) $\rightarrow NH_4^+$	^{15}N
Nitrifikation	$NH_4^+ \rightarrow NO_2^- \rightarrow NO_3^-$	^{15}N
Denitrifikation	$NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow$ — N_2O — N_2	^{15}N, ^{13}N
Dissimilatorische NO_3^--Reduktion	$NO_3^- \rightarrow NO_2^- \rightarrow NH_4^+$	^{15}N

[a] PON, partikuläre organische Stickstoffverbindungen; DON, gelöste organische Stickstoffverbindungen;

[b] zur Bestimmung der Proteinsynthese.

Abb. 5. Anwendungsmöglichkeiten von stabilen Isotopen bei der Untersuchung des Stickstoffmetabolismus insbesondere im marinen Ökosystem

Ergebnisse

In den folgenden Abschnitten werden die Resultate von Mikroalgen beschrieben, die in Massenkultur gehalten wurden. Da im marinen Ökosystem das Phytoplankton vor allem aus Diatomeen besteht, sind unsere Experimente vornehmlich an Reinkulturen von marinen Diatomeen durchgeführt worden. Im Vordergrund steht der Einfluss erhöhter UV-B-Strahlung auf Zellinhaltsstoffe (z.B. Pigmente, Proteine, Lipide) und auf den Kohlenstoff- und Stickstoffmetabolismus.

1. UV-B-Wirkung auf die Zellinhaltsstoffe von Mikroalgen

Der schädigende Einfluss der UV-Strahlung auf die Nukleinsäuren, Proteine und Pigmente von Planktonorganismen ist seit einiger Zeit bekannt (HALLDAL, 1979; WORREST, 1982). Dosiseffektkurven sind vom Pigment- und Proteingehalt mehrerer Arten von Mikroalgen ermittelt worden (DÖHLER, 1984a; DÖHLER et _al_., 1986). Als besonders UV-B-empfindlich erwiesen sich die

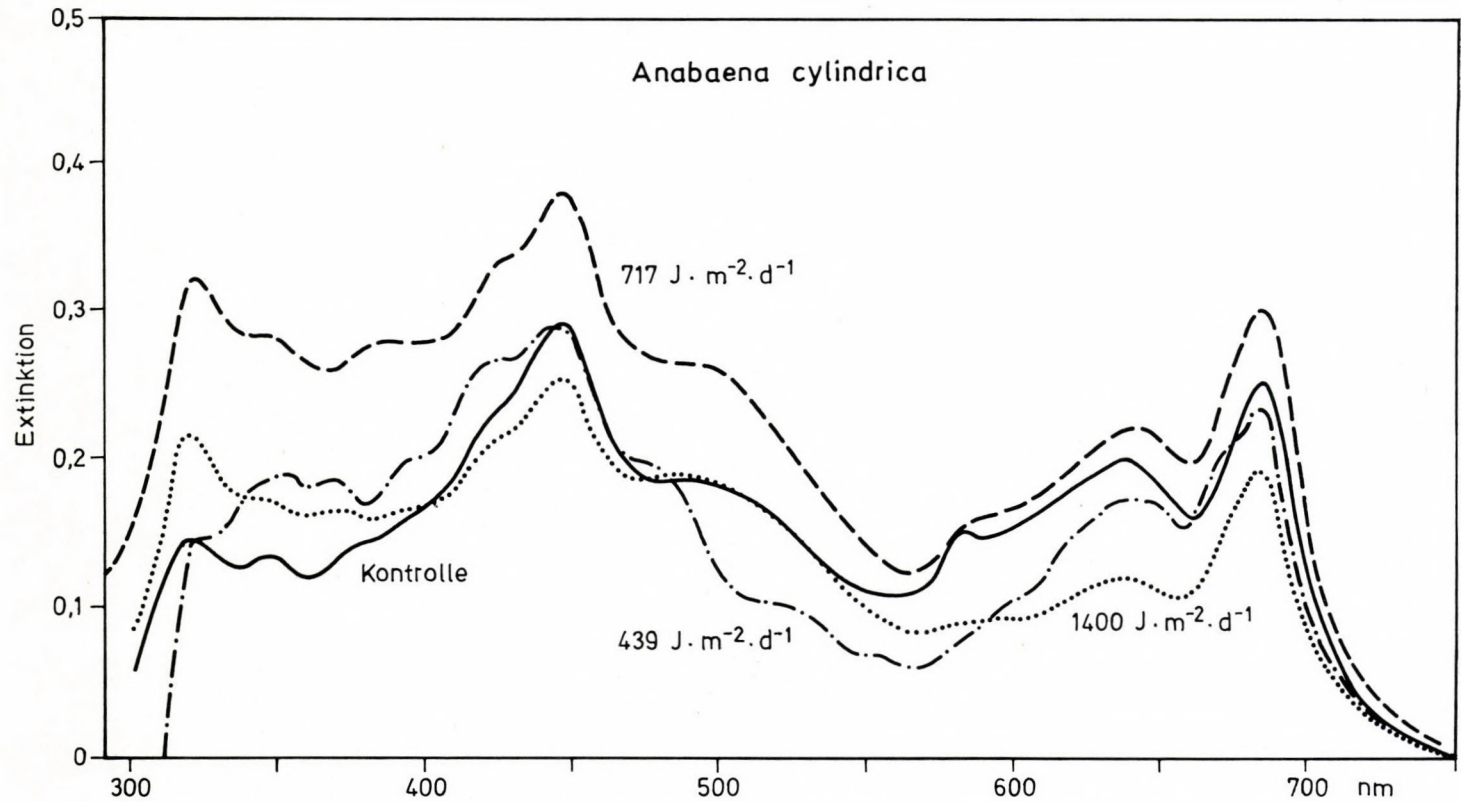



Abb. 6. Einfluss von UV-B-Strahlung verschiedener Intensität auf das Absorptionsspektrum von *Anabaena cylindrica*-Extrakten. Die UV-Dosis ist in J m^{-2} d^{-1} angegeben

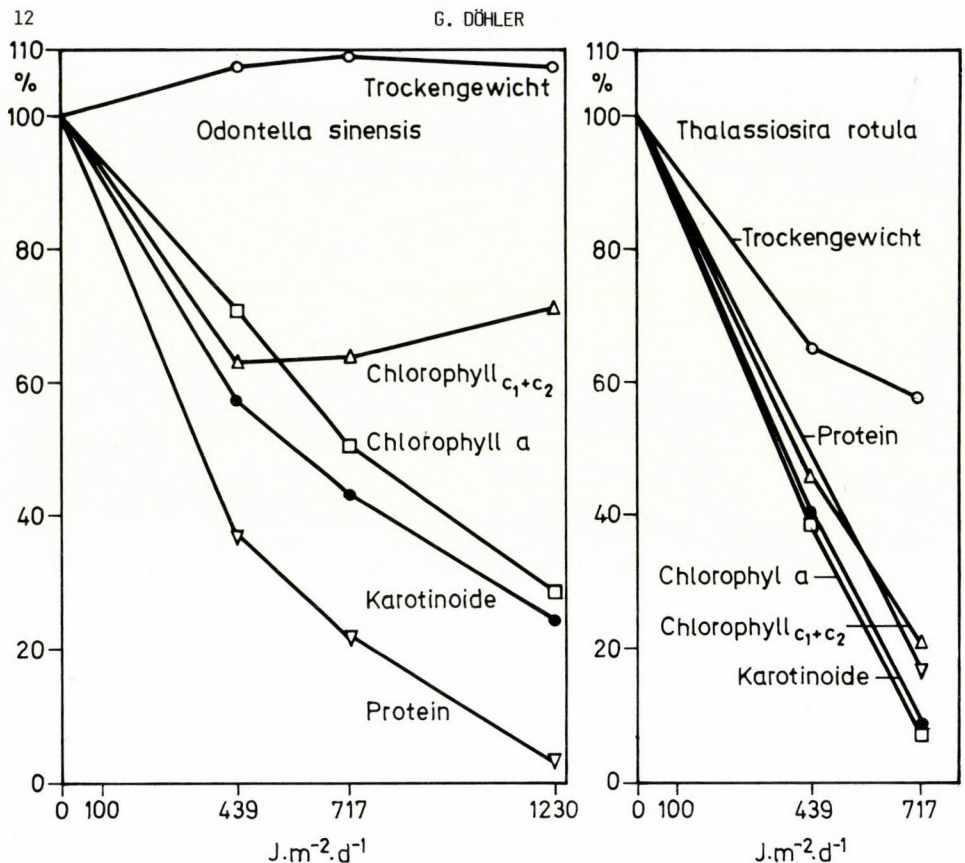



Abb. 7. Einfluss der UV-B-Strahlung verschiedener Intensität auf die Trockensubstanzmenge, den Chlorophyll a-, c_1+c_2-, Carotinoid- und Proteingehalt der Diatomeen Odontella sinensis und Thalassiosira rotula. Die Werte sind auf die nicht mit UV-B-bestrahlten Kontrollalgen bezogen und in % angegeben worden

Meeresdiatomeen, während die Cyanobakterien weniger sensibel waren. Bei den Cyanobakterien wurde nach UV-B-Bestrahlung eine drastische Reduktion des Phycocyaningehaltes beobachtet, was mit der Anordnung der Phycobilisomen auf den Thylakoidmembranen erklärt werden kann. Die Abb. 6 beinhaltet Absorptionsspektren der fadenförmigen Cyanobakterie Anabaena cylindrica, die mit verschiedenen UV-B-Intensitäten vorher bestrahlt wurde. Danach nehmen der Chlorophyll- und Phycocyangehalt entsprechend der Dosis ab. Besonders interessant ist der Anstieg des Absorptionsmaximums bei 320 nm, was offensichtlich auf ein UV-B-absorbierendes Pigment zurückgeführt werden kann. Ähnliche Beobachtungen wurden bei Synechococcus leopoliensis gemacht.

In einer Serie von Experimenten wurde die UV-B-Wirkung auf die Trockensubstanzmenge, den Pigment- und Carotinoidgehalt zahlreicher Diato-

Tabelle 1

Wirkung der UV-B-Strahlung verschiedener Intensität auf den prozentualen Anteil des Stickstoffs an der Gesamt-Trockensubstanz und dem Proteingehalt der Meeresdiatomeen Ditylum brightwellii, Lithodesmium variabile und Odontella sinensis

	Stickstoffgehalt						
	Kontrolle	439 J $m^{-2}d^{-1}$		717 J $m^{-2}d^{-1}$		1230 J $m^{-2}d^{-1}$	
Alge	N	N	% Hemmung	N	% Hemmung	N	% Hemmung
Ditylum brightwellii	3,25	3,07	5,5	2,18	32,9	1,53	52,9
Lithodesmium variabile	2,50	2,20	12,0	1,30	48,0	1,30	48,0
Odontella sinensi	1,20	0,85	19,2	0,81	32,5	0,98	18,3
	Proteingehalt						
	Kontrolle	439 J $m^{-2}d^{-1}$		717 J $m^{-2}d^{-1}$		1230 J $m^{-2}d^{-1}$	
Alge	mg/ml	mg/ml	% Hemmung	mg/ml	% Hemmung	mg/ml	% Hemmung
Ditylum brightwellii	0,196	0,095	51,5	0,060	64,4	0,0013	99,3
Lithodesmium variabile	0,096	0,079	17,7	0,060	37,5	0,0710	26,0
Odontella sinensis	0,037	0,014	63,0	0,005	86,8	0,0033	91,0

meenarten getestet. Repräsentativ für die erzielten Ergebnisse sind die Daten der Abb. 7. Danach wird die Biomasseproduktion durch UV-B weniger beeinflusst als der Pigment- und Proteingehalt. Ausserdem sind Unterschiede in der Reduktion der einzelnen Parameter je nach Algen- bzw. Diatomeenart gefunden worden. So waren die Grünalge Chlorella und die Rotalge Porphyridium bei gleicher UV-B-Dosis weniger geschädigt als die meisten Diatomeenarten. Andererseits konnte bei den Diatomeen ein art- und stadienspezifisches Verhalten gegenüber UV-B-Stress beobachtet werden. Die UV-B-Wirkung auf den Protein- und Stickstoffgehalt ist in der Tab. 1 für 3 Diatomeenarten zusammengefasst worden. Danach war Lithodesmium variabile weniger sensibel als Ditylum brightwellii und Odontella sinensis. Zusätzliche Stressfaktoren wie Temperatur und Salzkonzentration verursachen weitere Schäden in Kombination mit UV-B-Strahlung (DÖHLER, 1984b). So war das Ausmass der Reduktion des Pigment- und Proteingehalts in einer niedrigen Salzkonzentration (20‰) deutlich höher als in einer Salinität von 45 ‰. Die UV-B-Schäden waren bei der tropischen Diatomee Bellerochea yucatanensis in hohen Temperaturen niedriger als bei Diatomeen der gemässigten Zone; bei niedrigen Temperaturen wurde das umgekehrte Verhalten gefunden. Die bereits

bei niedrigen UV-B-Dosen festgestellt Beeinträchtigung des Wachstums und des Gehaltes an Nukleinsäuren konnte nach Licht- bzw. Dunkelphasen wieder repariert werden. Hohe Dosen, die durchaus bei einem normalen Sommertag auftreten können, führen zu irreversiblen Schäden.

Der Einfluss von UV-B-Stress auf die Synthese der Acyllipide wurde an Synchronkulturen der marinen Diatomee Ditylum brightwellii untersucht. Wenn zu Beginn der Lichtphase UV-B appliziert wurde, konnten - in Abhängigkeit von der Dosis - unterschiedliche Schäden bei den einzelnen Acyllipiden festgestellt werden. So wurde die stärkste Hemmung bei der Synthese von Digalactosyldiacylglycerin (DGDG) gefunden, während die Phosphatidylcholinsynthese (PC) nur geringfügig beeinträchtigt war. Die Synthese der anderen Lipide (Monogalactosyldiacylglycerin, MGDG; Phosphatidylglycerin, PC und Sulvoquinovosyldiacylglycerin, SQDG) waren bis zu 40 bzw. 70% reduziert und nahmen damit eine Mittelstellung im Vergleich zu den beiden anderen Lipidsynthesen ein. Ausserdem wurde eine unterschiedliche Reduktion durch UV-B bei den einzelnen Lipiden in Abhängigkeit vom Entwicklungsstadium der Ditylumzellen festgestellt. Keinen Einfluss hatte die UV-B-Strahlung während der Dunkelphase. Bei einer UV-B-Dosis von 780 J $m^{-2}d^{-1}$ war keine Induktion des Lipidabbaues nachweisbar (DÖHLER und BIERMANN, 1988). Durch UV-B-Bestrahlung trat auch eine Veränderung im Fettsäuremuster der einzelnen Lipide auf: Generell wurde ein Anstieg der längerkettigen Fettsäuren (C_{18}; C_{20}) und eine Verminderung der C_{14}/C_{16}-Fettsäuren beobachtet. Die Befunde werden mit einer Verminderung der Aktivitäten der entsprechenden Enzym erklärt, da z.B. die ATP-Synthese durch UV-B nicht beeinträchtigt war.

2. Die Wirkung der UV-B-Strahlung auf die Aufnahme von ^{15}N-Ammonium und ^{15}N-Nitrat

An Mikroorganismen sind die Aufnahme und Assimilation organischer und anorganischer Stickstoffverbindungen intensiv untersucht worden (LEA und MIFLIN, 1979; SYRETT, 1981; ULLRICH, 1983). Für den grössten Teil der Untersuchungen an Mikroalgen fanden spezielle Elektroden Anwendung. Die ^{15}N-Tracer-Technik ist von DUGDALE und GOERING (1967) bei der Erforschung der Assimilation ^{15}N-markierter Substanzen bei Phytoplankton eingeführt und von verschiedenen Arbeitsgruppen übernommen worden. Mit dieser Methode verfolgten COLLOS und SLAWYK (1979, 1980) den Einfluss verschiedener Stickstoffquellen und mehrerer äusserer Faktoren auf die Aufnahme ^{15}N-markierter Verbindungen bei marinem Phytoplankton. Seit einiger Zeit wenden wir diese Methode für Kurzzeitexperimente bei Mikroorganismen auch unter UV-B-Stress an.

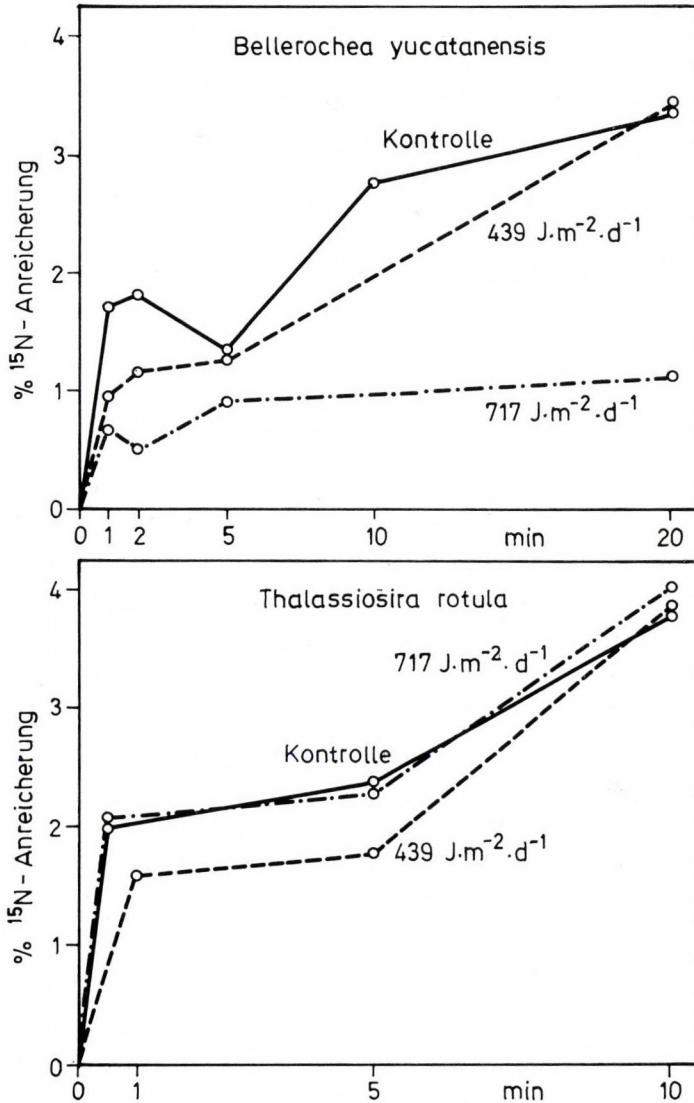



Abb. 8. Einfluss von UV-B-Strahlung (439 und 717 J $m^{-2} d^{-1}$, Wichtung nach Caldwell, 1971) auf die Kinetik der ^{15}N-Nitrataufnahme von Bellerochea yucatanensis und Thalassiosira rotula. Die Algen sind 2 Tage täglich 5 h mit UV-B bestrahlt worden; ein Parallelansatz in einer Glasröhre diente als Kontrolle. Die Anzuchts- und Versuchstemperatur betrug 18 ^{o}C. In einer speziellen Assimilationskammer aus Plexiglas sind den unterschiedlich vorbehandelten Algen nach 15 min Photosynthese ^{15}N-Nitrat (Endkonzentration 1 mM, 96,5 Atom%) zugegeben und die Proben nach verschiedenen Photosyntheseperioden entnommen worden. Für die weitere Prozedur siehe Material und Methoden

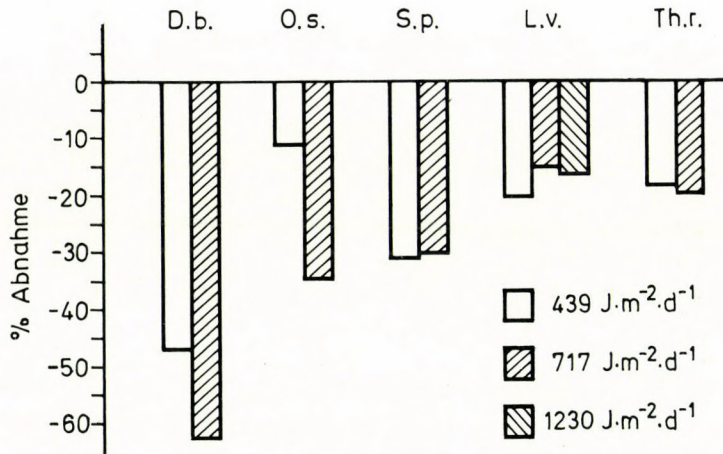



Abb. 9. Einfluss von UV-B-Bestrahlung auf die ^{15}N-Nitrataufnahme von mehreren Meeresdiatomeen nach einer Photosyntheseperiode von 10 min. Die Werte sind auf die der Kontrollalgen (nicht mit UV-B bestrahlt) umgerechnet und in % Abnahme angegeben. D.b. Ditylum brightwellii, O.s. Odontella sinensis, S.p. Synedra planctonica, L.v. Lithodesmium variabile, Th.r. Thalassiosira rotula. Weitere Angaben siehe Text

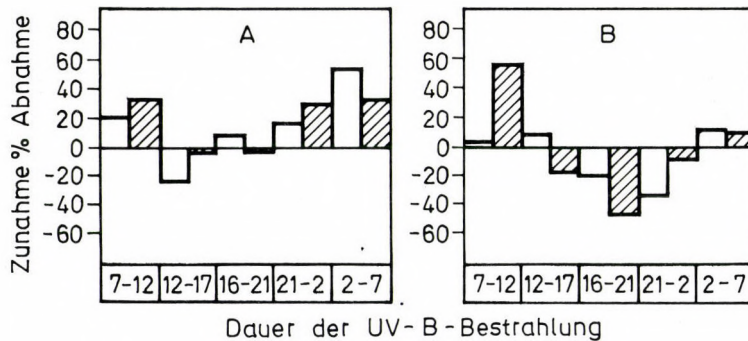



Abb. 10. Einfluss von UV-B-Strahlung (439 und 717 J $m^{-2}d^{-1}$) auf die photosynthetische Aufnahme von ^{15}N-Nitrat (A) und ^{15}N-Ammonium (B) von Ditylum brightwellii nach 10 min Photosynthese. Der Zeitpunkt der UV-B-Bestrahlung änderte sich im Tagesverlauf. Die Werte sind auf die der nicht mit UV-B-bestrahlten Algen bezogen und in % Ab- bzw. Zunahme dargestellt worden. ☐ 439 J $m^{-2}d^{-1}$, ▨ 717 J $m^{-2}d^{-1}$.

Die UV-B-Bestrahlung übt einen Einfluss auf den Transport, die Reduktion und Assimilation von organischen und anorganischen Verbindungen bei Mikroalgen aus. Eine Dosis-Wirkungsbeziehung konnte bei allen getesteten Cyanobakterien und Mikroalgen beobachtet werden (DÖHLER et al., 1986; DÖHLER und STOLTER, 1986). Als allgemeines Ergebnis kann festgehalten werden, dass die Aufnahme von ^{15}N-Ammonium gegenüber UV-B-Bestrahlung empfindlicher reagierte als die von ^{15}N-Nitrat. Bei den verschiedenen systematischen Gruppen (Cyanobakterien, Grün- und Rotalgen bzw. Diatomeen) wurde ein unterschiedliches Verhalten gegenüber UV-B-Bestrahlung gefunden, was sogar innerhalb einer Algengruppe - Diatomeen - zu beachten war. Diese unterschiedliche Reaktionsweise wird repräsentativ für alle anderen Ergebnisse in den Abb. 8 und 9 wiedergegeben. So wird die Kinetik der ^{15}N-Nitrataufnahme von Bellerochea yucatanensis entsprechend der UV-B-Dosis (439 und 717 J $m^{-2}d^{-1}$, Wichtung nach CALDWELL, 1971) weit stärker gehemmt als die von Thalassiosira rotula trotz gleicher Versuchsbedingungen. Dieser Befund war Anlass einer detaillierten Untersuchung über die UV-B-Wirkung bei unterschiedlicher Anzuchts- und Versuchstemperatur. Die ^{15}N-Nitrataufnahme der tropischen Diatomee Bellerochea yucatanensis wurde durch UV-B bei niedrigen Temperaturen (14-18 ^{o}C) stark reduziert, während bei einer Temperature von 26 ^{o}C nur ein geringer Effekt vorhanden war. Dagegen war bei Thalassiosira rotula eine hohe Temperatur in Kombination mit UV-B bereits lethal. An mehreren Diatomeenarten der gemässigten Zone (vor allem Isolate aus der Nordsee) wurde die UV-B-Wirkung auf die ^{15}N-Nitrataufnahme bei gleicher Anzuchts- und Versuchstemperatur (+18 ^{o}C) nach einem 2tägigen Wachstum bei täglich 5stündiger UV-B-Exposition getestet (Abb. 9). Nach einer Photosyntheseperiode von 10 min ist bei allen untersuchten Arten eine Reduktion der Nitrataufnahme gefunden worden, die je nach Art unterschiedlich war. Hierbei erwies sich Ditylum brightwellii als besonders sensibel, während die Aufnahmeraten von Lithodesmium variabile und Thalassiosira rotula deutlich weniger beeinflusst waren. Dieser Befund zeigt das artspezifische Verhalten gegenüber UV-B-Bestrahlung. Ausserdem können Unterschiede im Reaktionsverhalten der einzelnen Arten je nach vorausgegangener Beeinflussung durch andere Faktoren auftreten. Von besonderer Bedeutung ist hierbei der Zeitpunkt der UV-B-Einstrahlung während des Tages. Die Abb. 10 zeigt den Einfluss von UV-B auf die ^{15}N-Nitrat- (A) und ^{15}N-Ammoniumaufnahme (B) von Ditylum brightwellii nach 10 min Photosynthese. Bei Einstrahlung von UV-B während der Dunkelphase trat eine Steigerung der Aufnahmerate auf, während in der Lichtphase appliziertes UV-B in der Regel eine Hemmung verursachte. Als be-

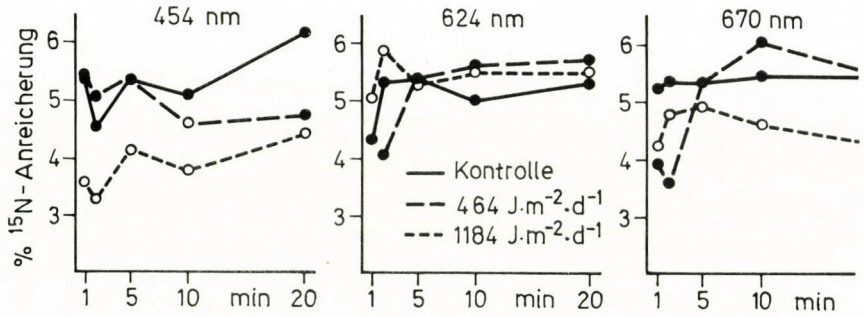



Abb. 11. Wirkung der UV-B-Strahlung (464 und 1184 J $m^{-2}d^{-1}$) auf die Kinetik der ^{15}N-Nitrataufnahme von Thalassiosira rotula bei gleichzeitiger Einstrahlung von monochromatischem Licht (454, 624 und 670 nm)

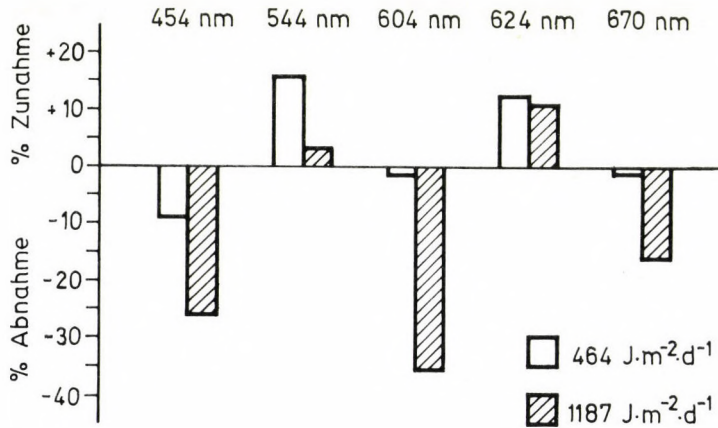



Abb. 12. Einfluss von UV-B-Strahlung (464 und 1184 J $m^{-2}d^{-1}$) auf die ^{15}N-Nitrataufnahme von Thalassiosira rotula nach 20 min Einstrahlung von monochromatischem Licht. Die Werte der ^{15}N-Anreicherung sind auf die der Kontrollalgen umgerechnet und in % Zu- bzw. Abnahme dargestellt worden

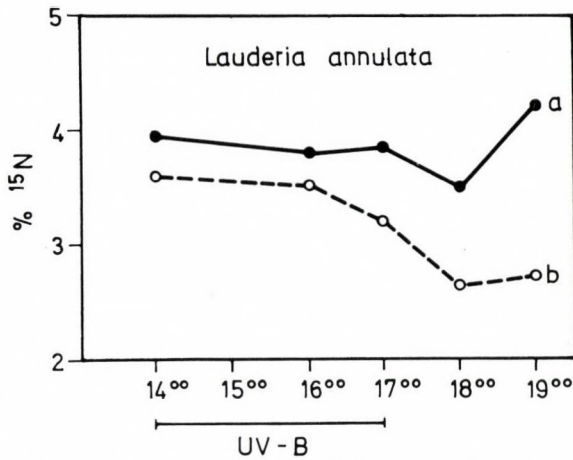



Abb. 13. Einfluss der UV-B-Bestrahlung (286 J $m^{-2}d^{-1}$) auf die ^{15}N-Nitrataufnahme von Lauderia annulata nach 5 min Photosynthese. a = 1. Versuchstag, b = 2. Versuchstag; die Werte sind in % ^{15}N-Anreicherung angegeben. Weitere Angaben in Material und Methoden

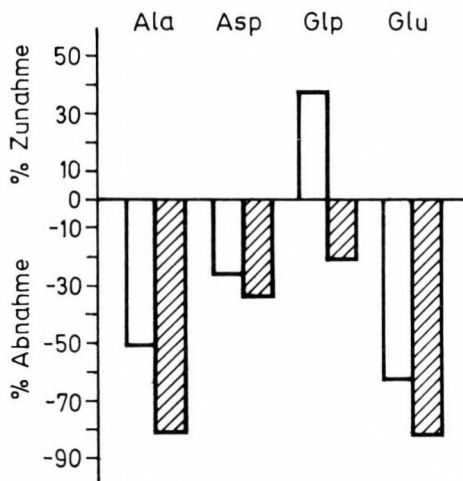



Abb. 14. Einfluss von UV-B-Bestrahlung auf den ^{15}N-Einbau in die Aminosäuren. Alanin (Ala), Aspartat (Asp), Glutamin (Gln) und Glutamat (Glu) von Ditylum brightwellii. Die Werte, 10 min nach Zugabe von $^{15}NH_4Cl$ (Endkonzentration 1 mM), sind auf die der nicht behandelten Zellen bezogen und in % Zu bzw. Abnahme angegeben.

□ 439 J $m^{-2}d^{-1}$, ▨ 717 J $m^{-2}d^{-1}$.

sonders empfindlich erwies sich die Aufnahme von $^{15}NH_4Cl$. Diese Befunde deuten auf eine stadienspezifische UV-B-Sensibilität hin, was an Synchronkulturen von Ditylum brightwellii für Lipide nachgewiesen wurde (DÖHLER und BIERMANN, 1988).

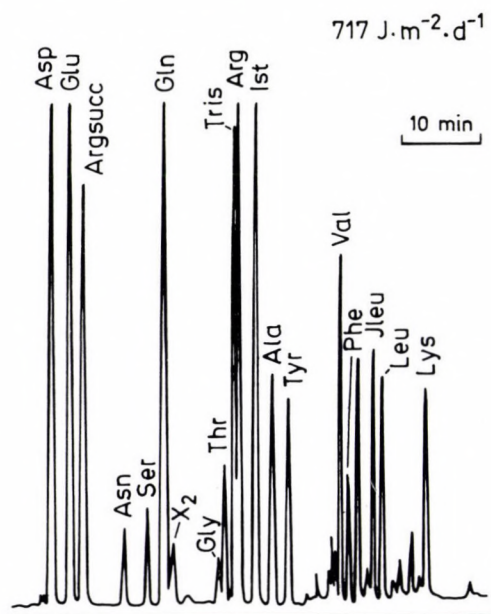
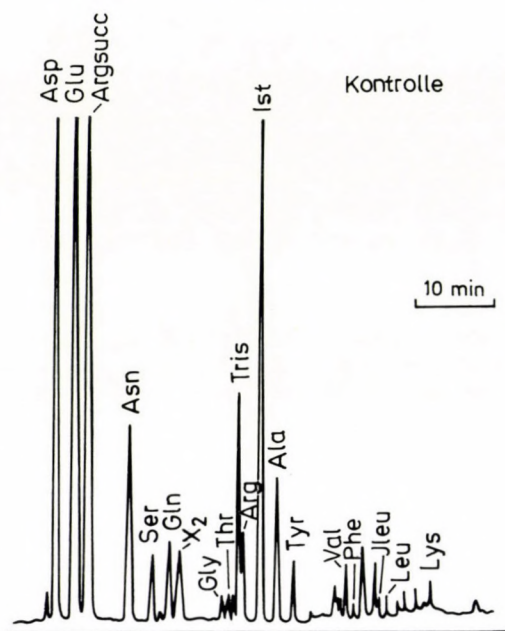
In einer anderen Serie von Experimenten ist die Wirkung von UV-B auf die ^{15}N-Nitrataufnahme von Thalassiosira rotula bei gleichzeitiger Einstrahlung von monochromatischem Licht untersucht worden (Abb. 11 und 12). Der Einfluss verschiedener UV-B-Intensitäten (464 und 1184 J $m^{-2}d^{-1}$) auf den zeitlichen Verlauf der ^{15}N-Nitrataufnahme bei Blau- (454 nm), Orangerot- (624 nm) und Rotlicht (670 nm) ist in Abb. 11 dargestellt. Danach führt UV-B im blauen und roten Bereich des Spektrums zu einer Verminderung der Aufnahmeraten entsprechend der UV-B-Dosis; demgegenüber wird im orangeroten Bereich eine Steigerung beobachtet. Die UV-B-Wirkung auf die ^{15}N-Nitrataufnahme von Thalassiosira rotula nach 20 min Bestrahlung mit monochromatischem Licht weist deutliche Unterschiede auf (vg. Abb. 12). Eine dosisabhängige Reduktion wird bei Blau-, Orange- und Rotlicht beobachtet. Dagegen tritt bei Grün- bzw. Orangerotlichtbestrahlung eine Zunahme auf. Die beobachtete Hemmung durch UV-B im blauen und roten Bereich des Spektrums kann mit den Absorptionsmaxima des Chlorophyll a in Verbindung gebracht werden. Eine Deutung der im grün- und orangeroten Licht gefundenen Steigerung der Nitrataufnahme kann derzeit nicht gemacht werden. Die Ergebnisse der UV-B-Wirkung auf die Ammoniumaufnahme von Thalassiosira rotula unter den gleichen Bedingungen stimmt mit denen von Nitrat weitgehend überein (DÖHLER und ALT, 1988).

Die Möglichkeit, durch UV-B hervorgerufene Schäden in der Aufnahme anorganischer Stickstoffverbindungen wieder aufzuheben, wurde an der marinen Diatomee Lauderia annulata geprüft (Abb. 13). Zu diesem Zweck sind die Algen 2 Tage in einer Quarzröhre kultiviert und täglich 3 h mit UV-B (286 J $m^{-2}d^{-1}$) bestrahlt worden. Am 1. Versuchstag konnte während der UV-B-Bestrahlungsdauer kein signifikanter Einfluss festgestellt werden; 1 h nach Abschluss der UV-B-Exposition trat eine reversible Hemmung der Nitrataufnahme auf (Abb. 13, Kurve a). Eine erneute Bestrahlung mit UV-B führte dagegen zu einer irreversiblen Schädigung der ^{15}N-Nitrataufnahme (Abb. 13, Kurve b). Diese Befunde deuten darauf hin, dass kurzfristiger UV-B-Stress reparabel ist.

3. UV-B-Wirkung auf den ^{15}N-Einbau in Aminosäuren und Proteine und auf die Poolgrössen der Aminosäuren

Die Untersuchungen der UV-B-Strahlung auf die Zellinhaltsstoffe haben ergeben, dass der Proteingehalt bereits nach niedrigen Dosen deutlich abnahm (DÖHLER, 1984a). Daher stellte sich die Frage, ob UV-B die Synthese der Aminosäuren und Proteine beeinträchtigt bzw. einen Abbau der Proteine induziert. Die ^{15}N-Markierung von Alanin, Aspartat, Glutamat und Glutamin der Alge Lauderia annulata änderte sich nach vorangegangener 2tägiger UV-B-Bestrahlung (5 h/Tag, 717 J $m^{-2}d^{-1}$): Der ^{15}N-Einbau in Glutamin stieg an und der in Aspartat und Glutamat nahm signifikant ab. Ähnliche Ergebnisse waren bei der Grünalge Chlorella fusca, der Rotalge Porphyridium purpureum und den Diatomeen Ditylum brightwellii und Thalassiosira rotula nachweisbar. Repräsentativ für diese ^{15}N-Experimente ist die Abb. 14. Die Verminderung des ^{15}N-Einbaues durch vorausgegangene UV-B-Bestrahlung war entsprechend der Dosis besonders drastisch bei Alanin und Glutamat. Bei einer UV-B-Intensität von 439 J $m^{-2}d^{-1}$ trat eine erhöhte ^{15}N-Markierung in Glutamin auf. Die Ditylumzellen, die dieser Dosis ausgesetzt waren, zeigten zu 50% eine Plasmolyse; bei einer höheren Dosis (717 J $m^{-2}d^{-1}$) wurde eine totale Plasmolyse gefunden. Auf Grund dieser Daten sind einige Schlüsselenzyme des Stickstoffmetabolismus getestet worden. So wurde die Aktivität der Alaninaminotransferase durch UV-B-Bestrahlung weit stärker geschädigt als die der Aspartataminotransferase (Hemmung von 90 bzw. 5%). Nach UV-B-Exposition nahm die Glutaminsynthetase-Aktivität um 15% zu und die Glutamatsynthetase-Aktivität war bis zu 40% vermindert. Zusammenfassend kann also festgehalten werden, dass die Befunde der ^{15}N-Experimente mit den Daten der enzymatischen Tests in Beziehung gesetzt werden können; d. h. es kann eine direkte Beeinflussung der Enzyme bzw. deren Synthese erfolgen. Ob die beobachteten Änderungen im Proteinmuster bei Ditylum brightwellii als Folge eines UV-B Einflusses mit den für die Enzymsynthese verantwortlichen Regulatorproteinen identisch ist, konnte noch nicht sicher festgestellt werden; niedermolekulare Proteinbanden fehlten.

In einer anderen Serie von Experimenten wurde der ^{15}N-Einbau in die Proteinfraktion von Ditylum brightwellii untersucht. Eine signifikante Reduktion ($\sim$ 30%) der Einbaurate trat bereits bei einer Dosis von 280 J $m^{-2}d^{-1}$ auf. Um die UV-B-Wirkung auf die Proteinsynthese zu prüfen, wurde der Einbau von ^{15}N-Leucin und 3H-Leucin unter Weisslicht- und UV-Bedingungen untersucht. In allen Versuchen wurde eine Reduktion des Leucin-Einbaues entsprechend der UV-Intensität nachgewiesen.

Bellerochea yucatanensis
Kontrolle
Asp
Glu
Argsucc
Ist
10 min
Asn
Tris
Ala
Ser
Gln
X2
Thr
Arg
Gly
Tyr
Val
Phe
Jleu
Leu
Lys
717 J.m-2.d-1
Asp
Glu
Argsucc
Gln
Tris
Arg
Ist
10 min
Val
Phe
Jleu
Ala
Tyr
Leu
Lys
Thr
Asn
Ser
X2
Gly

In Ergänzung zu den Tracer-Experimenten sind die freien Aminosäuren und Amide in Extrakten nehrerer Mikroalgen auch unter UV-B-Stress mittels HPLC getrennt und analysiert worden. Repräsentativ für die zahlreichen Analysen werden in Abb. 15 die Elutionsprofile von unbehandelten (Kontrolle) und mit UV-B bestrahlten (717 J $m^{-2}d^{-1}$) Bellerochea yucatanensis-Zellen dargestellt. Daraus geht hervor, dass die Poolgrössen z. B. von Glutamin, Alanin, Arginin, Valin stark ansteigen, während die von Glutamat, Argininosuccinat und Asparagin abnehmen. Die Resultate der Untersuchungen an zahlreichen Meeresdiatomeen sind in Abb. 16 tabellarisch zusammengestellt. Die Zunahme des Glutamin- bzw. die Abnahme des Glutamatpools wurde bei vielen marinen Diatomeen und Mikroalgen (Chlorella, Porphyridium) gefunden Dieser Typ 3 ist offensichtlich weit verbreitet. Bei Thalassiosira-Arten nimmt der Glutamatpool zu und der von Glutamin ab (Typ 2). UV-B führt in allen Fällen zu einer Zunahme des Aminosäurepools. Die Interpretation der erzielten Befunde ist in Abb. 16 enthalten und wird daher nicht erneut aufgeführt.

Nach den bisher vorliegenden Ergebnissen über den Transport, die Reduktion und den Einbau von NO_3^- und HN_4^+ ist der Weg des Stickstoffs in der Abb. 17 dargestellt worden. Bei dem aktiven Transport von Ammonium und Nitrat durch die Zellmembran wird Energie in Form von ATP verbraucht. Für die Reduktion von NO_3^- zu NO_2^- im Cytoplasma und von NO_2^- zu NH_4^+ im Chloroplasten werden Elektronen bzw. Reduktionsäquivalente ($NAD(P)H_2$ und Fd^{red}) benötigt. Bei den Diatomeen und anderen Mikroalgen kann Nitrat in der Vakuole gespeichert werden. Im Chloroplasten wird die Aminogruppe mittels Glutaminsynthetase (GS) unter ATP-Verbrauch auf Glutamat als Acceptor übertragen. Die Übertragung der Aminogruppe des gebildeten Glutamins auf α-Ketoglutarat katalysiert die Glutamatsynthase (GOGAT), wobei 2 Moleküle Glutamat entstehen und reduziertes Ferredoxin (Fd^{red}) verbraucht wird. Vom Glutamat ausgehend werden weitere Aminosäuren synthetisiert.

←

Abb. 15. Elutionsprofile der OPA-Aminosäuren aus Extrakten von Bellerochea yucatanensis. Die Algen wurden 2 Tage jeweils 5 h mit UV-B bestrahlt (717 J $m^{-2}d^{-1}$). Kontrolle = nicht mit UV-B behandelte Zellen. Ala: Alanin, Arg: Arginin, Argsucc: Argininosuccinat, Asn: Asparagin, Asp: Asparaginsäure, Gln: Glutamin, Glu: Glutaminsäure, Gly: Glycin, Ileu: Isoleucin, IST: interner Standard, Leu: Leucin, Lys: Lysin, Phe: Phenylalanin, Ser: Serin, Thr: Threonin, Tris: Tris (hydroxymethyl) aminomethan, Tyr: Tyrosin, Val: Valin, X_2: unbekannt

TYP 1	TYP 2	TYP 3
Wirkung:	Zunahme von	
Zunahme aller	Glutamat	Glutamin
Aminosäuren	Abnahme von	
	Glutamin	Glutamat
	und Verringerung von Aspartat und Asparagin	A: und Anstieg des Alaninpools. Interpretation: Hemmung der Glutamatsynthase und Alaninaminotransferase.
Interpretation:		
Hemmung der Proteinsynthese	Hemmung der Glutaminsynthetase und Phosphoenolpyruvat-Carboxykinase	Species: Lauderia annulata
		B: und Anstieg des Aspartatpools. Interpretation: Hemmung der Glutamatsynthase und Steigerung der Phosphoenolpyruvat-Carboxykinase.
Species:		
Chaetoceros debilis	Thalassiosira punctigera Thalassiosira rotula	Species: Asterionella glacilis Ditylum brightwellii
		C: und Reduktion des Aspartatpools. Interpretation: Hemmung der Glutamatsynthase und Phosphoenolpyruvat-Carboxykinase.
		Species: Bellerochea spinifera Bellerochea yucatanensis Odontella regia Odontella sinesis

Abb. 16. Zusammenfassung der mittels HPLC getrennten Aminosäuren und Amide von Meeresdiatomeen, die 2 Tage kultiviert und täglich 5 h mit UV-B bestrahlt wurden

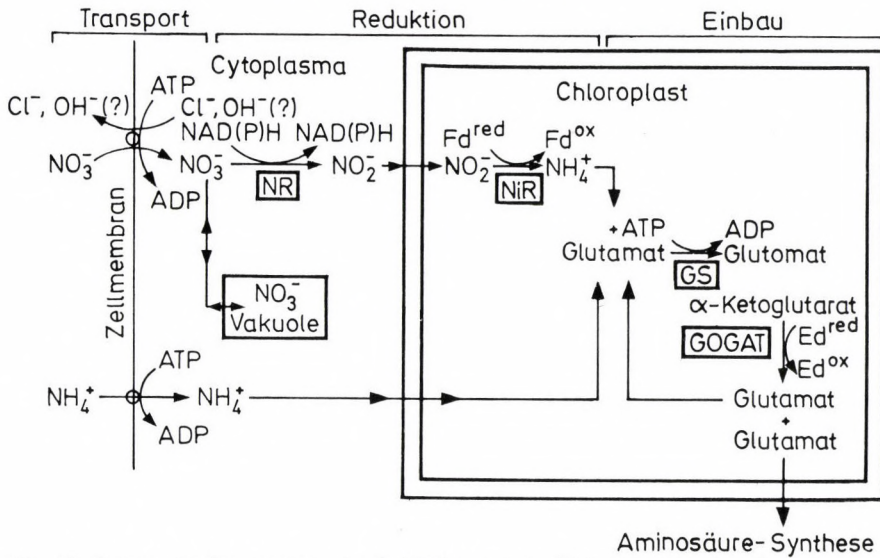



Abb. 17. Schema des Transportes, der Reduktion und des Einbaues von anorganischen Stickstoffverbindungen

4. UV-B-Wirkung auf den Kohlenstoffmetabolismus

Für den Stickstoffmetabolismus werden einerseits Energie und Reduktionsäquivalente und andererseits α-Ketosäuren für die Biosynthese der Aminosäuren benötigt (vgl. Abb. 3 und 17). In diesem Zusammenhang stellt sich die Frage, wo der primäre Angriffspunkt der UV-B-Strahlung liegt. Nach den bisher vorliegenden Untersuchungen wird das Reaktionszentrum des Photosystems II durch UV-B geschädigt, d. h. die Versorgung mit ATP und $NAD(P)H_2$ für die Stickstoffassimilation wird verringert (KULANDAIVELU und NOORUDEEN, 1983; IWANZIK et al., 1983). Eine weitere Beeinträchtigung der Assimilation von Stickstoffverbindungen kann über die Bereitstellung von Kohlenstoffverbindungen als Folge der UV-B-Bestrahlung auftreten. Aus diesem Grunde wurde die UV-B-Wirkung auf die photosynthetische CO_2-Fixierung und das Muster der Photosyntheseprodukte untersucht. Seit einiger Zeit ist bekannt, dass die Biomasseproduktion des Phytoplanktons durch den UV-Anteil der Sonnenstrahlung insbesondere nahe der Wasseroberfläche deutlich reduziert wird.

An den Cyanobakterien *Synechococcus leopoliensis* und *Anabaena cylindrica* ist der Einfluss einer vorausgegangenen UV-B-Bestrahlung (717 und 1405 J $m^{-2}d^{-1}$) auf die Kinetik der Gesamteinbaurate von ^{14}C-Bicarbonat gemessen worden. Die Wirkung von UV-B auf die Rate der CO_2-Fixierung von *Synechococcus* war gering. Dagegen wurde bei *Anabaena* eine entsprechend der

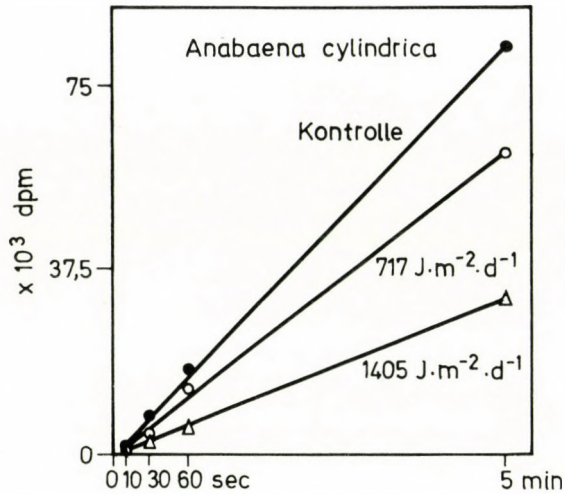



Abb. 18. Wirkung der UV-B-Bestrahlung verschiedener Intensität (717 und 1405 J $m^{-2}d^{-1}$) auf die photosynthetische $^{14}CO_2$-Fixierung von Anabaena cylindrica. Die Cyanobakterien wurden bei +22 °C unter Begasung mit atmosphärischer Luft (0,035 Vol. % CO_2) kultiviert und mit UV-B bestrahlt

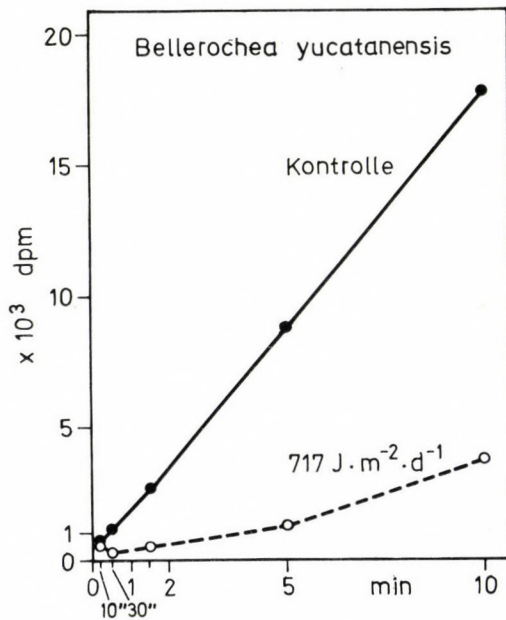



Abb. 19. Wirkung der UV-B-Bestrahlung (717 J $m^{-2}d^{-1}$) auf die photosynthetische $^{14}CO_2$-Fixierung von Bellerochea yucatanensis. Kontrolle = nicht mit UV-B bestrahlte Algen. Anzucht und Bestrahlungsbedingungen: +18 °C, 35‰ Salinität, 0,035 Vol. % CO_2, Licht/Dunkelwechsel 14:10 h und Weisslichtintensität 2600 Lux

UV-B-Dosis verminderte CO_2-Fixierungsrate gefunden (vgl. Abb. 18). Das Muster der ^{14}C-markierten Photosyntheseprodukte änderte sich bei den UV-B-behandelten Cyanobakterien nur geringfügig. Unsere bisher vorliegenden Ergebnisse zeigten, dass der Stickstoffmetabolismus gegenüber UV-B empfindlicher ist als die Assimilation des Kohlenstoffs (DÖHLER et al., 1986). NEWTON et al. (1979) fanden eine Schädigung der Nitrogenase während andere Prozesse nicht durch UV-B beeinträchtigt waren. Dieser Befund wird durch die Ergebnisse unserer enzymatischen Tests bestätigt (vgl. S...). Dies deutet darauf hin, dass UV-B-Strahlung die Enzyme des Kohlenstoff- und Stickstoff-Stoffwechsels in unterschiedlichem Ausmass hemmen.

Die photosynthetische CO_2-Fixierung von marinen Diatomeen erwies sich als wesentlich empfindlicher als die der Cyanobakterien nach vorausgegangener UV-B-Bestrahlung. Eine Dosis von 717 J $m^{-2}d^{-1}$ verursachte bei Bellerochea yucatanensis eine Plasmolyse aller Zellen und eine drastische

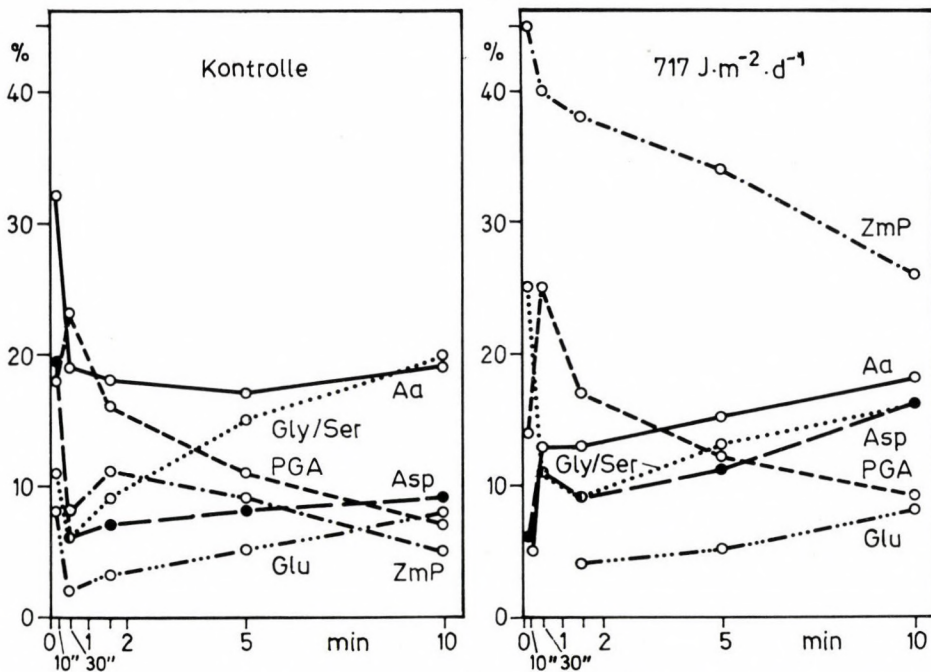



Abb. 20. Wirkung der UV-B-Strahlung (717 J $m^{-2}d^{-1}$) auf den ^{14}C-Einbau in verschiedene Photosyntheseprodukte von Bellerochea yucatanensis. ^{14}C-Bicarbonat wurde nach 15 min Photosynthese zugegeben; die ^{14}C-markierten Produkte sind dünnschichtchromatographisch getrennt worden. Anzuchtsbedingungen: +18 °C, 0,035 Vol. % CO_2, 2600 Lux Weisslichtintensität und 14:10 h Licht/Dunkelwechsel. Aa: gesamte Aminosäuren, Asp: Aspartat, Glu: Glutamat, Gly/Ser: Glycin/Serin, PGA: 3-Phosphoglycerinsäure und ZmP: Zuckermonophosphate

Hemmung der Gesamtfixierungsrate von ^{14}C-Bicarbonat (vgl. Abb. 19). In einem Parallelexperiment ist die Auswirkung der UV-B-Behandlung auf die Kinetik des ^{14}C-Einbaues in die löslichen Photosyntheseprodukte von Bellerochea yucatanensis verfolgt worden (Abb. 20). Aus dem Muster der prozentualen Verteilung der einzelnen Produkte geht hervor, dass die Radioaktivität in den Zuckermonophosphaten (ZmP) drastisch zunimmt, während die ^{14}C-Markierung der Aminosäuren - insbesondere von Glycin/Serin (Gly/Ser) und Glutamat (Glu) - deutlich verringert war. Dieses Ergebnis ist repräsentativ für die Untersuchungen an anderen marinen Diatomeen. Welche Bedeutung die Zunahme der Zuckermonophosphate in diesem Rahmen hat, kann noch nicht ausgesagt werden; es könnte sich hierbei um eine allgemeine Stressreaktion handeln.

5. Einfluss des UV-Anteils der Sonnenstrahlung auf die Assimilation anorganischer Stickstoffverbindungen eines Diatomeen-Gemisches und natürlicher Phytoplanktonpopulationen

Bisher wurde nur über die Auswirkungen von UV-B-Bestrahlung auf die Zellinhaltsstoffe und den Zellstoffwechsel von marinen Diatomeen berichtet, die als Reinkulturen unter Laborbedingungen mit UV bestrahlt wurden. Da diese Versuche mit Unialgalkulturen durchgeführt wurden, können keine Aussagen über die Wechselbeziehungen zwischen den einzelnen Arten in einem Gemisch bzw. im Plankton gemacht werden. In Vorversuchen mit einer Algengemeinschaft, bestehend aus mehreren Diatomeenarten, ist bei einigen Species ein anderes Verhalten gegenüber UV-B-Bestrahlung im Vergleich zu den Unialgalkulturen beobachtet worden. Wenn Reinkulturen von Phytoplanktonarten z. B. Skeletonema costatum, Chaetoceros debilis, Prorocentrum micans den natürlichen Bedingungen des Meeres ausgesetzt waren, konnten nahe der Wasseroberfläche Auswirkungen der Sonneneinstrahlung festgestellt werden, die mit den unter Laborbedingungen erzielten UV-B-Effekten weitgehend identisch waren. Diese Beobachtungen waren der Anlass für eine detailliertere Untersuchung unger Freilandbedingungen.

Zu diesem Zweck wurde die Aufnahme von ^{15}N-Ammonium und ^{15}N-Nitrat eines Diatomeen-Gemisches (Ditylum brigthwellii, Lithodesmium variabile, Odontella sinensis, Thalassiosira rotula) während des Tagesverlaufs ermittelt. Um die Wirkung des UV-Anteils der Sonnenstrahlung zu erfassen, fanden UV-transparente Plexiglasgefässe Verwendung. In einem Parallelversuch wurden UV-nichtdurchlässige Plexiglasgefässe für das Algengemisch benutzt

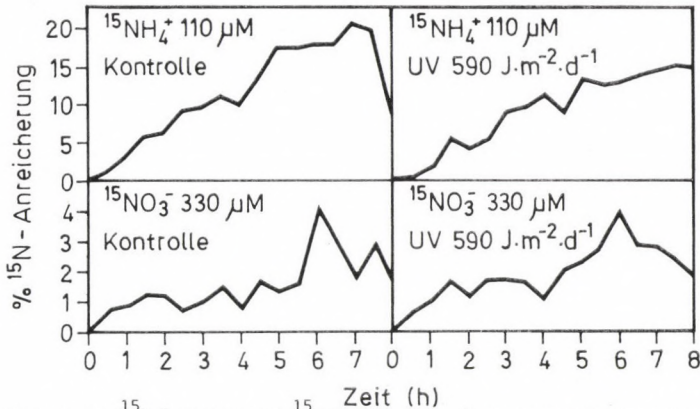



Abb. 21. Aufnahme von ^{15}N-Ammonium und ^{15}N-Nitrat eines Diatommeengemischs unter dem Einfluss der natürlichen Sonnenstrahlung. Die Tagesdosis des UV-Anteils betrug 590 J m^{-2}d^{-1} und die Tagestemperatur 16-18 ^{o}C. Weitere Angaben siehe Material und Methoden

(Kontrollalgen). Je nach den Wetterbedingungen traten Unterschiede in den Intensitäten der Sonnenstrahlung und damit des UV-Anteils auf, die entsprechende Auswirkungen auf die Aufnahme der anorganischen Stickstoffverbindungen zur Folge hatten. Repräsentativ für die erzielten Ergebnisse ist in Abb. 21 der Einfluss einer UV-Dosis von 590 J m^{-2}d^{-1} auf den Tagesverlauf der $^{15}NH_4^+$- und $^{15}NO_3^-$-Aufnahme dargestellt worden. Danach trat keine Veränderung in der Nitratassimilation auf. Dagegen war eine Reduktion der Ammoniumaufnahme feststellbar. Eine höhere Dosis des UV-Anteils der Sonnenstrahlung führte auch zu einer Verminderung der Nitrataufnahme. Da die Auswirkungen des UV auf den Stickstoffmetabolismus der einzelnen Arten nicht erfasst werden können, wurde das Wachstumsverhalten der Diatomeenarten unter den natürlichen Bedingungen in UV-transparenten und UV-undurchlässigen Plexiglasgefässen ermittelt. Entsprechend der Dosis des UV-Anteils der Sonnenstrahlung verringerte sich die Wachstumsrate von Thalassiosira rotula und die von Ditylum brightwellii nahm zu. Danach war in dem Algengemisch Thalassiosira rotula UV-empfindlicher als Ditylum brightwellii. In der Unialgalkultur wurde nach UV-B-Bestrahlung das umgekehrte Verhalten beobachtet. Unsere Befunde zeigen, dass eine Erhöhung der UV-Intensität unter Freilandbedingungen unterschiedliche Schäden bei den einzelnen Arten hervorrufen und somit das Artengefüge eines Ökosystems verändert werden kann.

In zahlreichen Experimenten wurde die Assimilation des Planktons an den Küsten Südnorwegens und Helgolands in verschiedenen Wassertiefen verfolgt. Je nach Lichtverhältnissen wurde nahe der Wasseroberfläche in der Regel eine niedrigere Aufnahmerate des Planktons in den Quarzflaschen im

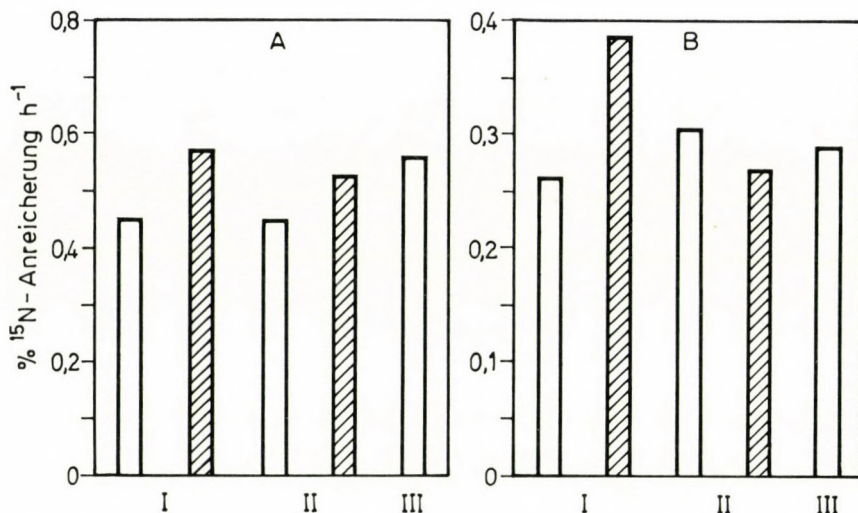



Abb. 22. Die Aufnahme von ^{15}N-Ammonium (A) und ^{15}N-Nitrat (B) von natürlichen Phytoplanktonproben in Abhängigkeit von der Meerestiefe. I 0,17 m; II 1,17 m; III 2,67 m Meerestiefe. ☐ UV-transparente, ▨ UV-undurchlässige Plexiglasgefässe. Die Beleuchtungsstärke betrug für Experiment A 133 J m^{-2} h^{-1} und für B 209 J m^{-2} h^{-1}. Weitere Angaben in Material und Methoden

Vergleich zu den Proben in Glasflaschen gefunden. In tieferen Wasserschichten traten nur geringe Unterschiede auf oder es wurden in den UV-transparenten Gefässen höhere Werte gemessen (vgl. Abb. 22). Trotz unterschiedlicher Arten-Zusammensetzung der photoautotrophen Organismen in der Phytoplanktonpopulation wurden zu den verschiedenen Jahreszeiten im Prinzip die gleichen Effekte beobachtet: Die Ammoniumaufnahme war empfindlicher als die Nitrataufnahme. Vor allem nahe der Wasseroberfläche wurde eine Hemmung der Aufnahmeraten festgestellt, da in tieferen Wasserschichten durch vorhandene Partikel die UV-Strahlung absorbiert bzw. gestreut wurde. In Abb. 22 ist die Wirkung des Sonnenlichts auf die Ammonium- und Nitrataufnahme des Phytoplanktons in verschiedenen Wassertiefen dargestellt worden. Daraus geht hervor, dass bereits niedrige Intensitäten eine Reduktion der ^{15}N-Ammoniumaufnahme verursachen (Abb. 22, A), während erst bei höherer UV-Dosis die Nitrataufnahme vermindert wird (Abb. 22, B). Wenn statt Planktonproben Reinkulturen den gleichen natürlichen Bedingungen ausgesetzt werden, treten die gleichen UV-Schäden auf. Ähnliche Beobachtungen wurden ebenfalls an Makroalgen gemacht.

In einer anderen Serie von Experimenten ist die Wirkung des natürlichen UV-Anteils der Sonnenstrahlung auf den ^{15}N-Einbau in mehrere Aminosäuren untersucht worden (Tab. 2). Unter annähernd gleichen Bedingungen

Tabelle 2

Einfluss des UV-Anteils der Sonnenstrahlung auf den ^{15}N-Einbau in verschiedene Aminosäuren von natürlichem Plankton und Reinkulturen von Prorocentrum micans und Skeletonema costatum. Nach Zugabe von $^{15}NH_4Cl$ (1 mM Endkonzentration; 96,0 Atom%) wurden die Proben in Glas- bzw. Quarzflaschen in 1 m Wassertiefe exponiert. Das Plankton bestand zu 90% aus Ceratium fusus. Die Werte sind in % ^{15}N-Anreicherung und die Lichtintensität in W m^{-2} angegeben. G: Glas- und Q: Quartzflaschen. Weitere Details siehe Material und Methoden

Lichtintensität		Alanin	Aspartat	Asparagin	Glutamat	Glutamin
			natürliches Phytoplankton			
G	335	0,53	0,62	-	1,39	1,47
Q	335	0,29	0,33	-	1,19	1,82
			angereichertes natürliches Phytoplankton			
G	691	1,39	6,94	-	3,12	24,08
Q	691	0,50	10,73	-	3,28	23,13
			Prorocentrum micans			
G	230	1,47	1,52	6,86	4,05	4,86
Q	230	4,55	10,78	18,80	8,68	31,79
			Skeletonema costatum			
G	663	4,57	33,92	42,00	15,42	75,74
Q	663	1,33	25,60	37,77	4,93	76,03

fanden hierzu natürliche Planktonproben und Reinkulturen der Phytoplanktonarten Prorocentrum micans und Skeletonema costatum Verwendung. Die ^{15}N-Markierung von Glutamin war stets höher als die von Glutamat, was auf eine Assimilation des Stickstoffs nach dem Glutaminsynthetase/Glutamatsynthase-Weg hindeutet. Die relativ hohe ^{15}N-Anreicherung in Alanin und Aspartat kann mit einer CO_2-Fixierung nach der β-Carboxylierungsreaktion interpretiert werden. Dies stimmt mit den Ergebnissen von KREMER und BERKS (1978) und Rosslenbroich und DÖHLER (1982) überein. Die bei natürlichem Phytoplankton und Skeletonema costatum beobachtete Reduktion des ^{15}N-Einbaues in Alanin und Aspartat geht offensichtlich auf eine Hemmung der entsprechenden Aminotransferasen durch den UV-Anteil zurück. Auf Grund unserer Untersuchungen an Reinkulturen beeinträchtigt die UV-B-Strahlung die Enzymaktivitäten in unterschiedlicher Weise.

Diskussion

Die Ergebnisse der vorliegenden Arbeit haben gezeigt, dass UV-B-Bestrahlung die Pigmentierung, den Proteingehalt und die Biomasse-Produktion der Mikroalgen, insbesondere bei hohen Dosen, deutlich beeinträchtigen. Bei natürlichen Phytoplanktonpopulationen wurde von mehreren Autoren eine deutliche Beeinträchtigung des Pigmentgehaltes durch den UV-Anteil der Sonnenstrahlung beobachtet (WORREST, 1982). UV-B-Schäden wurden sowohl bei Proteinen als auch bei der DNA - aufgrund des Absorptionsverhaltens - festgestellt (HALLDAL, 1979). Niedrige UV-Intensitäten bzw. kurze Expositionsdauer führten in der Regel zu reparablen Schädigungen. Besonders auffällig ist das art- und stadienspezifische Verhalten der Mikroalgen gegenüber UV-B-Bestrahlung (vgl. DÖHLER, 1984a; WORREST, 1982 und dort aufgeführte Zitate). Das unterschiedliche Verhalten der Organismen kann einerseits auf die Zugehörigkeit zu verschiedenen taxonomischen Gruppen (vgl.Abb. 1) und andererseits auf die unterschiedlichen Standortbedingungen zurückgeführt werden.

Das unterschiedliche Ausmass der Reduktion von Zellinhaltsstoffen und des Zellstoffwechsels der Mikroalgen hat Auswirkungen auf das Wachstum der einzelnen Arten und damit auf das Artengefüge im Ökosystem. Eine Veränderung der Artenzusammensetzung als Folge von UV-B-Stress kann negative Einflüsse auf die Nahrungskette haben. Von Untersuchungen an Phytoplankton ist bekannt, dass fadenförmige Cyanobakterien weit weniger durch UV geschädigt werden als z. B. die Diatomeen (CALKINS und THORDARDOTTIR, 1980). Diese Beobachtung wird durch unsere Arbeiten an Mikroalgen bestätigt. Die Diatomeen, die den Hauptbestandteil des Phytoplanktons darstellen, sind als Primärproduzenten von grosser Bedeutung und erwiesen sich als besonders UV-B-empfindlich. Die Veränderungen im Artengefüge können positive Auswirkungen haben, wenn die dominierenden Arten eine gute Nahrungsquelle für die Primärkonsumenten sind. Die Regel ist jedoch die Dominanz schlecht verwertbarer bzw. toxischer Arten (z. B. Cyanobakterien), sodass eine Reduktion oder Schädigung der Konsumenten in der Nahrungskette zu erwarten ist. Demnach wird eine Erhöhung der Intensität der UV-B-Strahlung und eine Verlagerung zum kürzerwelligen Bereich des Sonnenspektrums - infolge des Ozonabbaus - zu Veränderungen in den biologischen Systemen und der Nahrungskette führen.

Eine Reduktion der stratosphärischen Ozonschicht und damit verbunden die Verminderung der Biomasseproduktion der höheren Pflanzen auf dem

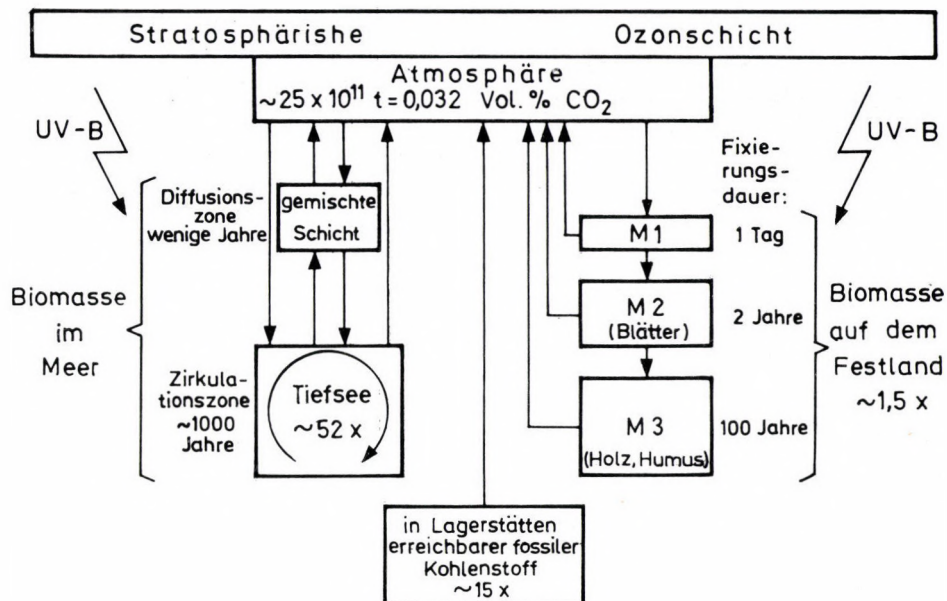



Abb. 23. Schema der Reservoire und Austauschwege des Kohlenstoffs (verändert nach Wagener und Förstel) und die Auswirkungen der Reduktion der Biomasseproduktion durch erhöhte UV-B-Strahlung als Folge des Ozonabbaues. Der fixierte Kohlenstoff beträgt in der Biomasse des Festlandes das 1,5-fache, in den fossilen Lagerstätten das 15-fache und in der Tiefsee das 52-fache der Atmosphäre

Festland und der Plankton-Organismen im Meer kann das Gleichgewicht zwischen dem CO_2-Gehalt der Atmosphäre und den in den Organismen und im Meer gebundenen Kohlenstoff erheblich stören (Abb. 23). Durch die verringerte Biomasseproduktion der Pflanzen werden die Austauschwege des Kohlenstoffs deutlich beeinträchtigt. Von besonderer Bedeutung sind die Meeresorganismen, da im Meer ca. 55 mal mehr Kohlendioxyd gelöst als in der Atmosphäre vorhanden ist. Wenn die CO_2-Fixierung des Phytoplanktons z. B. durch UV-B stark reduziert wird, kann weniger atmosphärisches CO_2 im Meer gelöst werden, da der Partialdruck des CO_2 durch das Lösungsgleichgewicht festgelegt ist. Die Störung der Durchmischungs- bzw. Fixierungsdauer des CO_2 dürfte einen geringen Anstieg des CO_2-Gehaltes der Atmosphäre zur Folge haben. Die Verbrennung des in den Lagerstätten verfügbaren Kohlenstoffs bewirkt ebenfalls eine Zunahme des CO_2-Gehaltes. Ein Anstieg der CO_2-Konzentration in der Atmosphäre führt zu dem sogenannten "Treibhaus-Effekt", d. h. eine Erhöhung der Temperatur auf der Erdoberfläche, was zu drastischen Klimaveränderungen und teilweise zum Abschmelzen der Polkappen führen kann.

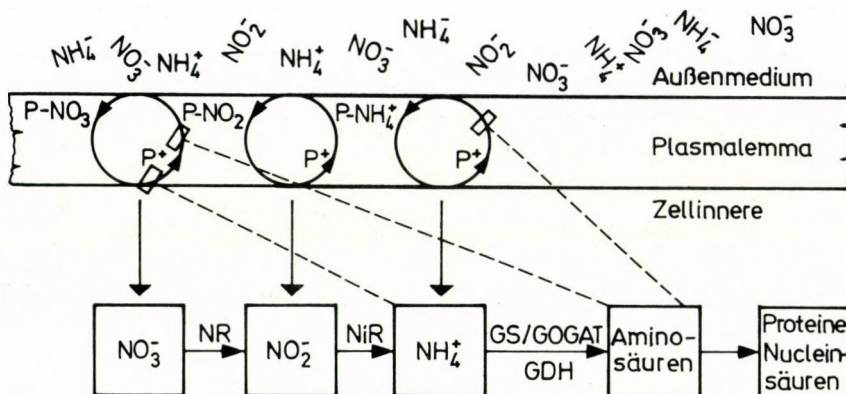



Abb. 24. Vereinfachtes Schema der Aufnahme anorganischer N-Verbindungen und deren mögliche Regulation (verändert nach CONWAY, 1977)

Unsere Untersuchungen über den Einfluss der UV-B-Strahlung auf den Stickstoffmetabolismus und die photosynthetische CO_2-Fixierung haben ebenfalls gezeigt, dass die Reaktion der Mikroalgen art- und stadienspezifisch ist. Die Aufnahme- bzw. Assimilationsraten nahmen entsprechend der UV-B-Dosis ab (Dosis-Effekt-Kurven; vgl. Abb. 18 und 19). Die Aufnahmerate von ^{15}N-Ammonium war gegenüber UV-B-Stress empfindlicher als die von ^{15}N-Nitrat. Zusammenfassend kann festgehalten werden, dass bei Reinkulturen von Mikroalgen, Phytoplanktonalgen und Makroalgen praktisch das gleiche Verhalten beobachtet wurde. Die gefundenen Effekte waren weitgehend identisch unabhängig davon, ob die Messung während der UV-B-Bestrahlung oder einige Zeit danach erfolgte. Als Erklärungen für die beobachtete Reduktion der Aufnahme anorganischer Stickstoffverbindungen durch UV-B kommen in Frage:

1. UV-B kann direkt die Lipide und Proteine der Membranen schädigen und damit das Transportsystem der Stickstoff-Verbindungen,

2. die Hemmung des Reaktionszentrums des Photosystems II durch UV-B kann eine Verminderung der ATP-Versorgung zur Folge haben (KULANDAIVELU und NOORUDEEN, 1983),

3. die geringere Rate der photosynthetischen CO_2-Fixierung und/oder Atmung dürfte zu einer verminderten Bereitstellung von Kohlenstoffverbindungen für die Aminosäuresynthese führen,

4. die UV-B-Strahlung kann Änderungen im Regulationsmechanismus der Aufnahme anorganischer Stickstoff-Verbindungen bewirken,

5. ein direkter Einfluss von UV-B auf die Schlüsselenzyme des Stickstoff-Metabolismus (z.B. über Schäden der Protein bzw. RNS/DNS) ist ebenfalls denkbar.

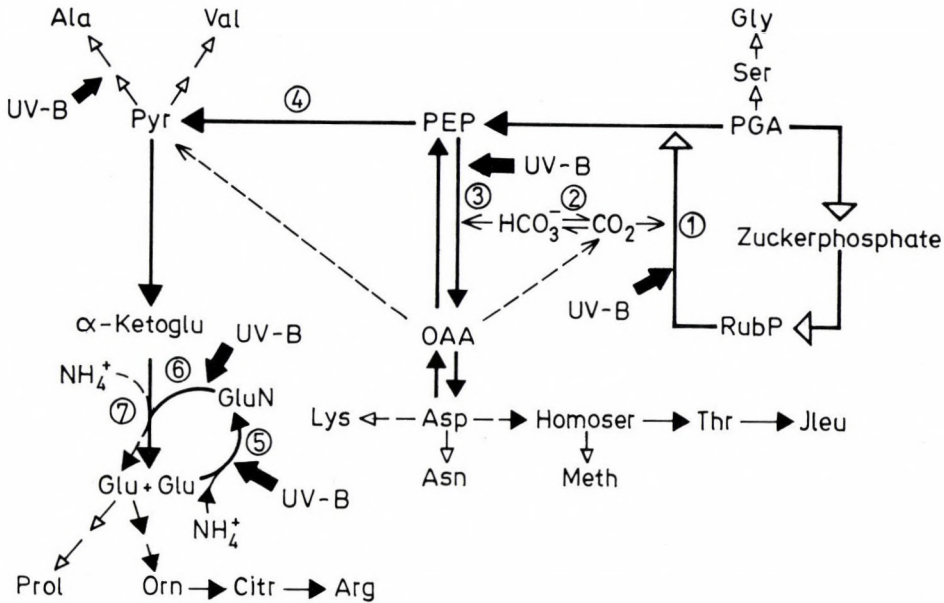



Abb. 25. Schema des Kohlenstoff- und Stickstoffmetabolismus von Mikroalgen und der vermutete UV-B-Einfluss. 1 Ribulose-bisphosphatcarboxylase, 2 Carboanhydrase, 3 Phosphoenolpyruvat-carboxylase/-carboxykinase, 4 Pyruvatkinase, 5 Glutaminsynthetase, 6 Glutamatsyntase und 7 Glutamat-Dehydrogenase

Die beobachtete Hemmung der Acyllipid-Synthese nach bzw. während der UV-B-Bestrahlung kann durchaus eine Veränderung in den Membranen zur Folge haben und auf diese Weise das Transportsystem beeinträchtigen (Abb. 24). Die Verfügbarkeit von ATP wurde durch UV-B nicht vermindert, was entsprechende Messungen zeigten. Dagegen dürfte die Hemmung der CO_2-Fixierung durchaus einen Einfluss auf die Aminosäurebiosynthese über die Bereitstellung von Kohlenstoffskeletten haben. Allerdings wurde eine Reduktion der Assimilation von Stickstoff-Verbindungen bei relativ niedrigen UV-B-Dosen beobachtet, die keinen Einfluss auf den Kohlenstoff-Metabolismus ausübten. Bei allen Mikroalgen wurde eine Veränderung im Pool der Aminosäuren und Amide nach Bestrahlung mit UV-B beobachtet; bei zahlreichen Arten trat eine Erhöhung des Glutamin-Pools auf. Da Glutamin offensichtlich für die Regulation der Stickstoff-Aufnahme von Bedeutung ist, wird auf diese Weise der Transport anorganischer Stickstoff-Verbindungen beeinflusst (vgl. Abb. 24). Die bisher vorliegenden Befunde zeigen, dass die Wirkung von UV-B auf die Aufnahme anorganischer Stickstoff-Verbindungen vielfältig ist. Über den primären Angriffspunkt und den entscheidenen Parameter können zur Zeit noch keine exakten Angaben gemacht werden.

Enzymatische Untersuchungen ergaben, dass die Enzyme des Kohlenstoff- und Stickstoff-Metabolismus in unterschiedlichem Masse gehemmt werden. So wurde die Aktivität der Ribulose-bisphosphatcarboxylase stärker beeinträchtigt als die der Phosphoenolpyruvatcarboxykinase. Die gleiche UV-B-Dosis bewirkte bei der Glutaminsynthetase (GOGAT) eine Aktivitätssteigerung von 15-20%, während die Glutamatsynthase-Aktivität um 40% abnahm. NEWTON et al. (1979) fanden eine spezifische Hemmung der Nitrogenase-Aktivität von Anabaena flos-aquae bei einer UV-B-Intensität, die zu keinen anderen Schäden führte. Dieser Befund und unsere Ergebnisse deuten daraufhin, dass UV-B die Enzyme bzw. die Enzymsynthese direkt beeinträchtigen kann. Die Abb. 25 beinhaltet die möglichen Angriffspunkte von UV-B auf die Enzyme des Kohlenstoff- und Stickstoff-Metabolismus. Weitere Untersuchungen sind notwendig um detailliertere Informationen über die UV-B-Wirkung auf den Stoffwechsel von Mikroorganismen zu erhalten.

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Acta Botanica Hungarica 35(1-4), pp. 39-54 (1989)

THE DISCIPLINAR ROOTS AND SOME POSSIBLE INTERPRETATIONS OF THE LIFE-STRATEGY CONCEPT IN THE LICHENOLOGY

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(Received 15 November 1988)

All kind of researches in the lichenology and overall in ecology should be based on the aspiration to show up the manifold behaviour of the living organisms. The author has came to the conclusion that the scientific background of this kind of concept was originated from the works of GAMS and MATTICK. Their manysided concept, concerning coenology, ecology and physiognomy was called as an Austrian-German or Central European School of physiognomical ecology. The role of the taxonomy in the life-strategy concept was emphasized because all descriptions should be in correlation with taxonomy. Matrices and transitional schemes were used for the interpretation of the transitions between the different dissemination, growth form, and life-strategy - types, on the basis of 10 years investigations.

Introduction

Although the notion "life-strategy" became an often used term in the ecology, its disciplinar roots have not been lightened in a really exact way.

It seems that one of the most important reasons of this situation comes from the fact that this concept was usually adopted as an "unifying approach" (e.g. GRIME, 1983). As GRIME has written: "Strategies may be defined as groupings of similar or analogous genetic characteristics which recur widely among species or populations and cause them to exhibit similarities in ecology."

It is no doubt that this kind of "arrangement" of living organisms could be very spectacular but it has plenty of traps, too. Which are these traps, and where do they come from? This study deals with the lichenological aspects but it appears to author that the following list has of moments for general meaning, too:

1. In consequence of the "unifying" ambitions the taxonomy was highly neglected by the ecologists. Besides the brilliant works of POELT

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(e.g. 1969, 1974a, b, etc.) and WIRTH (e.g. 1987) the lichenology is very short of reliable summaries in the taxonomy.

2. The life-strategy concept comes from the knowledge of the life cycles. The latter must be based on unambiguous taxonomic descriptions which are hold the phenetical sides of the genetical background.

3. It is no doubt that the above-mentioned points have not been lightened properly in the lichenology, and with some exceptions (e.g. WILMANNS, 1987), it is true for the whole botany. (For instance the life-strategy concepts written by McARTHUR and WILSON, 1967; PIANKA, 1970 and GRIME, 1974, 1977, etc.). These ideas were not adopted by lichenologists first of all because of the lack of the similarities between the flowering plants and lichens. The same has happened with the publications of STEARNS (1976) and WILBUR et al. (1974) and WILBUR (1976) although these studies have already took care of manysided behaviour of living organisms. Latter has stated that the "life history strategy" consist of several components among which are reproductive effort, reproductive life span, age of first reproduction and many other attributes.

4. The quantitative view was predominated nearly in all articles dealing with strategies, against the qualitative descriptive approaches. The qualitative characterisation of the lichen colonies or communities are closely related to the taxonomy and it has particular importance in the bioindication. The colour and the shape, or the pruinosity of lichen thalli wears important taxonomical and ecological informations (DU RIETZ, 1924; WEBER, 1962, 1967, 1977; GILBERT, 1974; POELT, 1974a, b; SEAWARD, 1976; KISS, 1982, 1985, 1987).

5. It is very pleased to know about the increasing number of articles dealing with the ecophysiological side of the strategies. This field has great future (e.g. SMITH and MOLESWORTH, 1973; TÜRK, WIRTH and LANGE, 1974; FARRAF, 1978; SMITH, 1979; SEAWARD, 1980; AHMADJIAN and JACOBS 1983; TÜRK, 1983 etc.).

This very short introduction has also proved that the life-strategy concept needs a renewal, firstly from taxonomical and morphological points of views faced towards a thorough qualitative analyse.

What are the roots of the life-strategy concept in the lichenology?

The best answer for this question to recall or to bring back the ideas of the pioneer thinkers in our mind. The starting point was the "growth- or life-form" concept.

The essence of this new way of thinking was, that it was able to bring together such notions as morphology, physiognomy and ecology. GAMS (1932) has written that the growth forms and life forms are "ecological units", and "life forms can be classified either morphologically, physiognomically and ecologically". GAMS has made "an attempt at a purely ecological classification of all plants and animals as a basis for a completely natural and general system of vegetation". It was not an unifying approach. On the contrary, GAMS always wanted to show the world in its great diversity, but he knew well that living organisms are able exist only within "societies", so "the most useful groupings are those which characterize whole societies". He was always against the unnatural classifications of natural communities. It is high time to confess that he has won with his synusia-concept in the cryptogamic biology and coenology, too, and because of the forced application of the Braun-Blanquet method we have no useful coenological system in the lichenology till now. Unfortunately neither the works of GAMS (1918, 1932), nor the important papers of MATTICK (1937, 1951) have not been taken into consideration for a long time. However, MATTICK's (1951) statements have played outstanding role in the elaboration of the life-strategy system of lichens (KISS, 1985).

Let's see some quotations from his main work: "... die Wuchsformen zwar innerhalb der Gattung verschieden, aber für die einzelnen Arten festliegend und daher zu artdiagnostisch verwertbaren Eingeschaften geworden, so können sie andreseits sogar innerhalb einer Art noch schwankend sein, z. B. bei den zahlreichen Standorts-Modifikationen der Cladonien...". Another one: "War für die Gruppierung von Pflanzen nach Wuchsformen nur der Habitus entscheidend, so erkannte man nun, dass der Einfluss des Lebensraums in der Aufstellung von Lebensformen zum Ausdruck gebracht werden kann." "Die Flechten als Haftpflanzen reagieren, wie GAMS hervorgehoben... viel schäfer auf die ökologischen Faktoren als die wurzelnden Pflanzen." "... die feinsten Indikatoren dar für physikalische und chemische Einwirkungen."

"Ähnlich wie eine Phanerogamgesellschaft eine reiche Schichtung zeigen kann, ist das auch im kleinen gesehen bei den Flechtengesellschaften

möglich. Sie können ein-, zwei- oder dreischichtig sein: die einschichtigen Gesellschaften setzen sich entweder nur aus Krustenflechten, nur aus Laubflechten, oder nur aus Strauchflechten..." He has elaborated an "ökologisch-physiognomischen System", in which "... Lebensformen und Substrat zugrunde gelegt, und man kann dann die Lebensformen und die entsprechenden Gesellschaften in zwei parallel laufenden Systemen neben einander stellen (vgl. GAMS, 1918, S. 471.!)." About successions: "Die Flechtengesellschaften lassen noch manche andere Betrachtungsweise zu z. B. eine syngenetische Klassifikation; diese stellt fest, ob die untersuchten Gesellschaften Anfangstadien, Übergangs- oder Endstadien... Ferner ob sie Initialphasen, Optimalphasen oder Degenerationsphasen darstellen..." "GAMS hat 1918 auf derartige Sukzessionsreiben aufmerksam gemacht, z. B. an den Vogelsitzplätzen, oder die rhytmische Folge der baumbewohnenden Flechten-Gesellschaften vom Aufwachsen des Baumes bis zum Vermodern des Stammes. - Auch eine Anordnung nach der soziologischen Progression ist möglich..."

The clear distinction between the notions of growth- and life-form, the vertical stratification of the lichen communities on the basis of their growth forms, an "Ökologisch-physiognomischen System" using the life- and growth forms of the colonies, an attempt for the elaboration a new coenosystem on ecological background, and the recognition that the growth forms are not as "stabile structures" as it was thought, and last not least the dynamical and sociological conceptions, which were at the highest conceptual level at that time.

During the historical researches it has cleared up that amongst the well-known coenological and ecological schools - e.g. Zürich-Montpellier, the school of Clements, etc. - an Austrian-German, or Central European School was also on the stage of the science, founded by GAMS and MATTICK, and it is still existing in our days. At the beginning of our century this school seemed to be the so-called "golden way" between the extreme views within the coenology and ecology.

GALLÉ (1976-77) has become one of the Hungarian representatives of this school with his coenological work. Otherwise the Hungarian lichenology was also originated from the above analysed ideas, bringing many new valuable and interesting results (e.g. FELFÖLDY, 1942, 1943; GALLÉ, 1930, 1960, 1971; SZATALA, 1939; VERSEGHY, 1983, etc.). On the other hand, the dates of the above-mentioned articles show that the roots of this school have already existed in the Hungarian coenology, too. That is why the "Central European" name.

Between GAMS and MATTICK — in the meantime — has come Du RIETZ (1924) with his valuable publication about the "Soredien und Isidien der Flechten". This article was also one of the main bases of the life-strategy concept in the lichenology.

He put many interesting questions and brought plenty of examples in connection with the production of soredia and isidia.

Taxonomy played important role in his ecological thinking. Some examples are given here only: one of the most interesting questions he put: "... in welchem Grade die Soredien- und Isidienproduktion phänotypisch modifizierbar ist, eine Frage...". And an example: "... kenne ich eine sehr grosse Menge von Fällen wo die Mengenverhältnisse der Soredien- und Isidienproduktion sehr stark modifizierbar sind".

Another interesting question: "Sind die soredien-(resp.isidien-) losen und die Soredien-(resp.isidien-)produzierenden Formen scharf getrennt oder nicht?"

He observed that "... dass normal reich soredienproduzierende Arten unter gewissen Standortsverhältnissen schwach soredienproduzierende Modifikationen ausbilden können. Alle solche Fälle lassen sich aber durch Naturbeobachtungen ganz leicht aufklären." It is one of the main tasks of the life-strategy researches, too. He continued with another problem: "Eine andere Frage ist der Einfluss der Standortsverhältnisse auf die Reichlichkeit der Soredien-/resp.Isidien-/Produktion bei einer soredien- oder isidientragenden Art." On the basis of field works he has established, that "... kenne ich viele Fälle, wo eine Art unter dem Einfluss von unreiner Luft (in der Nähe des Städte etc.) eine abnorm starke Soredien- oder Isidien-produktion aufweist (z.B. Physica orbicularis, Ph. nigricans, Xanthoria fallax, Parmelia furfuracea, Usnea hirta)".

The presence or absence, and the density of isidia, soredia or apothecia became useful phenetical signs in the bioindication of the level of air pollution (e.g. PYATT, 1974; KISS, 1984, etc.). Recently, BAILEY (1976) has brought many new results on this topic. As a result of field works it has cleared up that the morphological performances (SEAWARD, 1976) or environmental modifications (POELT, 1974; WEBER, 1977) have crucial importance in the monitoring of different environmental stresses.

As POELT (1974) has pointed out: "Lichens lack the capacity to develop special resting stages for survival during unfavourable periods. Thus, as long-lived organisms, they may be subjected to the effects of an extreme and hostile environment over a period of many years. This leads to

considerable environmentally induced modification, and the range of phenotypic variation."

Figure 1summarizes the disciplinar roots of the life-strategy concept, including the well-observable responses of lichens and the possible types of interpretations.

These roots have put this concept in action in the plant physiology, too. The most important from these is the concept of "physiological buffering", elaborated by SMITH and MOLESWORTH (1973) and SMITH (1979). By the way, all studies dealing with lichen physiology recall the brilliant fundamental work of BUTIN (1954), because of its "Ökophysiologische..." ground.

The first life-strategy system in the cryptogamic ecology was elaborated for the bryophytes by JOENJE and DURING (1977) and DURING (1977), calling back the concept of GAMS', quoted above.

Abbreviations: A = area of populations (cm^2 or mm^2); A_r = reproductive area of populations (cm^2 or mm^2), and the ratio of them: $\frac{A}{A_r}$.

Fig. 1. Disciplinar roots of the life-strategy concept

What does mean the notion of life-strategy in our renewed concept?

1. First of all,it is a manyfold approach, investigating the different kinds of responses of the organisms.

2. This concept dates back to the coenological physiognomical and dynamical concepts of the so-called "Central European School" of physiognomical ecology.

3. In consequence of these disciplinar roots this kind of life-strategy concept is more flexible than the rigid categorization and has not so much extreme than the "holocoenotic" concept (like the ecosystem concept).

4. By this concept we try to regard the things through the "eyes" of the organisms, in our case that of the lichens.

5. This life-strategy concept does not build hedges between the different levels of organizations; namely, between individuals, populations and communities. The responses must be investigated in all the above-mentioned levels.

6. In the applied methods and in the interpretation of the results we have to take care of the ideal balance between the qualitative and quantitative approaches (See Fig. 1!).

7. In the life-strategy researches, the sensory perception ought to stand on the first place. In other words: we have to detect the phenetical signs, those signs which are easy to recognize at the site, and at the same time these signs express different kind of responses of the investigated organisms. This is the "manyfold approach".

8. In spite of the"unifying approach" the main peculiarity of this life-strategy concept is demonstrating the manysided behaviour of the living organisms.

Interpretations

The life-strategy system of lichens — elaborated by the author (KISS, 1985) — based on the combinations of the growth forms and the types of disseminations of the species. These phenetical attributes reflect on many kind of responses of the species or populations, which have outstanding importance in the bioindication. The main responses are following:

1. The possible and realized combinations of the dissemination types of the species.

2. Degrees of environmentally induced modifications.

3. Changes of the growth-forms and in the dissemination types, or transition into each other.

4. Changes in fertility.

5. Growth rates of populations.

6. Trends of succession.

The last two (5. and 6.) needs exact measurements for many years. All above-mentioned features are applicable on the level of individuals, populations and coenoses of lichens.

Table 1 shows the possible combinations of the four fundamental types of disseminations.

Table 1

Combinations of the four fundamental types of disseminations

	So	Is	Sp	Tf
So	-	(So+Is)	(So+Sp)	(So+Tf)
Is	(Is+So)	-	(Is+Sp)	(Is+Tf)
Sp	(Sp+So)	(Sp+Is)	-	(Sp+Tf)
Tf	(Tf+So)	(Tf+Is)	(Tf+Sp)	-

Abbreviations: Is = isidium; So = soredium; Sp = spore; Tf = thallus fragment

In this symmetrical matrix the pairs of dissemination types are not equal with each other.
For example: (Is+So) ≠ (So+Is), which means:

Is>So and So>Is.

The exact meaning of this case that - in our instance - the observed thalli are dispersed better either by isidia or soredia. The quantitative interpretation of this situation is possible with the measure of A_r of the thalli or population. A_r is the reproductive area of the lichen populations. It means the cover values (in cm^2 or mm^2) of isidia, soredia and apothecia existing on the surface of the thalli. The density of dispersal propagules on the surface of the thalli and the types of the propagules or the state of the propagules are in a very close connection with the level of air pollution.

Some examples of the extinction of the thalli on the basis of dissemination:

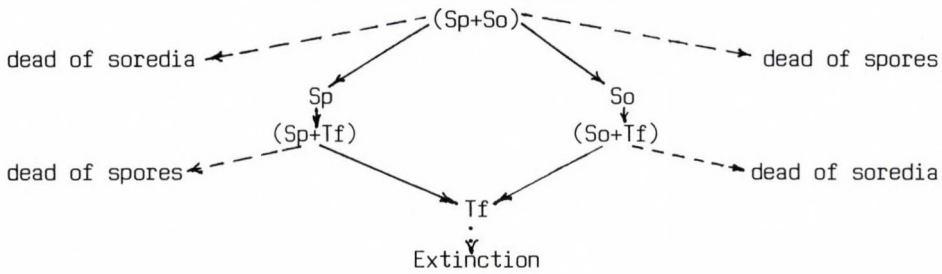
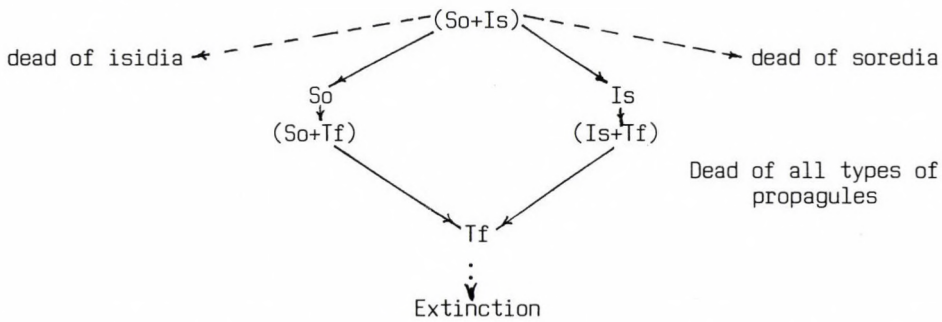
a.)

b.)

Naturally these are only few examples from the possible variations of the destructions and extinctions of the thalli by the dead of the sexual and asexual propagules.

Table 2 represents some observed transitions between the growth-form types in the case of degeneration and development of the thalli:

Table 2

	Sf	Lf	Fr	Thr	Ba	Cl
Sf	-	+	+			+
Lf	+	-			sector of development	
Fr	+	+	-			
Thr				-		
Ba		Sector of degeneration			-	
Cl	+					-

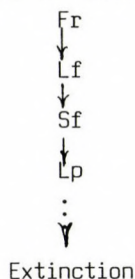
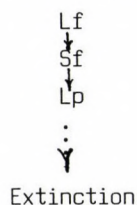
Abbreviations: Sf = small foliose; Lf = large foliose; Fr = fruticose; Thr = threadlike, Ba = Baeomyces type, Cl = Cladonia type.

+ = P_{ij}, where i an j are the different growth form types. P_{ij} means the possibility of the transition of the P_i growth form into the growth-form of j, within the period of t+1. The replacement between the identical growth forms is not possible because of their identical histology.

The possibility of the transition or performance of the growth-form i, into the j one - or vice versa - is depend on the abundance (for example the number of colonies, etc.) of i and j types within a locality, e.g., in a forest or on the bark of a tree.

The transition of a growth-form type into another one is a very slow process because of the slow growth rate of the colonies. On the other hand, the degeneration of a growth-form type, and in consequence of this, the performance into another one is usually a more rapid process. It depends on the level of the air pollution and on the speed of its change.

These performances could be expressed on the individual and population level.

Some examples with the aim of transitional schemes

The starting point of the development of a species is always a small piece of thallus without any dissemination propagules. It is true also in those cases when this small pieces of thallus is an isidium or part of an isidium or only a little soredium. The process towards the Tf types is considered as the path into a degenerated state. There are two exceptions, when the thallus fragments is originated from soredia or isidia. In these cases the So $\rightarrow$ Tf, or So $\rightarrow$ Tf So and the transitions of Is $\rightarrow$ Tf or Is $\rightarrow$ Tf $\rightarrow$ Is are possible. Performances from Tf towards the (So+Tf),

(Sp+So), (So+Is), (Is+Sp), (Is+Tf) and (Sp+Tf) types express the development of vegetative diaspores or spores.

Table 3 gives some possible life-strategy types using the combinations of dissemination types and growth-forms.

Table 3

	Lp	EndCr	EpCr	Sf	Lf	Fr	Thr	Ba	Cl
So	W			X	W				
Is				X	W				
Sp		W	W	X	W			W	
Tf		D	X	X	X	X	X		X
(So+Is)				X	W				
(So+Sp)			W						W
(So+Tf)			X	D	X	W			
(Is+Sp)									
(Is+Tf)				D	D	W	W		
(Sp+Tf)				D					

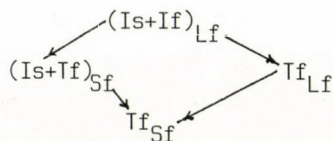
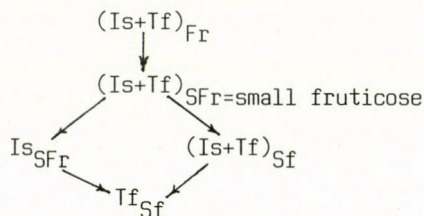
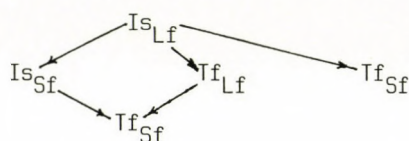
The meaning of marks: W = well-developed types; X = some transitional states; D = degenerated types.

Let's give some examples on the basis of Table 3.

So_{Sf} was considered as a transitional type which means that it could be a transition towards the large foliose (Lf) type, but at the same time it may be the degenerated types of the So_{Lf}, too. Tf_{Sf} represents another step towards the extinction of a thallus or thalli, but in the reverse situation — for instance in a biotic succession — this is the first type of the foliose colonies, in other words: this is a juvenile thallus type.

Here arises a question: How can we detect the orientation of the transitions?

The e is no other way for it but continuous longer observation, by permanent sampling units.

Performances between different life-strategy types using transitional schemes:

These kind of performances leads usually to the extinction of the thalli.

Let's see some examples about the development of colonies:

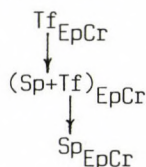
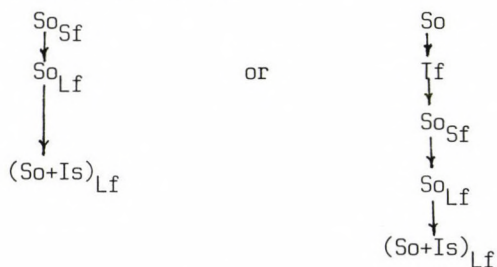
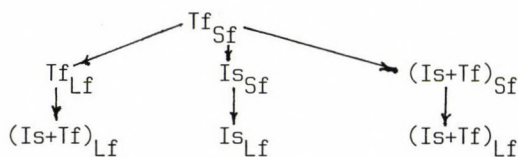
a.)

Tf_{EpCr}

↓

$(Sp+Tf)_{EpCr}$

↓

Sp_{EpCr}

In this case the areoles will be overgrown by apothecia and the dispersal propagules will be the spores.

Point b.) shows that the starting points could be soredia or small pieces of thalli wearing soredia.

Point c.) exhibits some possible parallel ways.

These performances shed light to the different phases of the successions and give exact informations about the trends, too (KISS, 1982, 1985).

It must be emphasized that the above-mentioned examples consist of only a small part of possible and observed combinations between different life-strategies, or dissemination types which were studied in Western Hungary between 1979 and 1988.

Summary

The fundamental roots of a renewed life-strategy concept of the lichens were discussed in some details.

The main points were following:

1. This life-strategy concept was originated from the so-called "Austrian-German"- or "Central European School of physiognomical ecology".

2. In spite of the "unifying approach" the importance of different disciplinar roots — including taxonomy and morphology — were emphasized.

3. It was stated that the ideal balance between the quantitative and qualitative aspects has crucial importance, both in the methods and in the interpretations, as well.

4. On the basis of 10 years investigations — in the region of West Hungary — some possible transitions between different life-strategy types were interpreted with the use of matrices and transition schemes.

5. This grasp of life-strategy concept contains many kinds of responses which have great importance in the environmental monitoring (e.g. dissemination spectra and their changes, modifications, fertility, etc.).

6. All features, exhibited by lichens, are applicable on the level of individuals, populations and coenoses.

7. Contrary to the often used "short-therm" or "quick" methods in the monitoring of air pollution, it was showed that only the long-term researches give exact and useful results in the field of bioindication.

Acknowledgements

I am grateful to Dr. P.K. VERSEGHY for her valuable and helpful suggestions, and Prof. Dr. ROMAN TÜRK for the interesting discussions during my stay at the University of Salzburg in 1988, and to Dr. Z. SZŐCS for his many helpful opinions.

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Acta Botanica Hungarica 35(1-4), pp. 55-71 (1989)

LICHENS AS INDICATORS OF AIR POLLUTION IN THE BUDAPEST AGGLOMERATION II. ENERGY DISPERSIVE X-RAY MICROANALYSIS OF HYPOGYMNIA PHYSODES (L.) NYL. THALLI

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Hypogymnia physodes (L.) Nyl. thalli were collected (together with the supporting bark) from four localities in Hungary in Budapest and in the Pilis Mountains NW from Budapest and studied using SEM-EDXRA methods. The surface, dorsal cortex, gonidial layer, medulla, ventral cortex and the supporting bark were analysed separately. Presence of Na, Mg, Al, Si, P, S, Cl, K, Ca, Ti, V, Fe, Co, Ni, Cu, and Zn was detected and measured in various areas of the thalli. The studied anatomical structures showed considerable differences in their element composition and the same is true for thalli taken at different localities. Medullary hyphae showed extreme thickening of cell walls caused by deposition of Ca-containing material(s). Analyses of the ventral cortex of thalli and the underlying bark yielded very close results suggesting that the primary absorbentis the bark and thalli take up the concentrated materials from there. Data were subjected to principal component analysis, cluster analysis and rank correlation analysis according to Spearman.

Introduction

While hundreds of papers have been published on the special organic substances produced by lichens (see reviews by CULBERSON, 1969, 1970; CULBERSON et al., 1977), element content of lichens, location of elements in thalli, cycling of nutrient elements by lichens seem to be much less known (BROWN, 1976; ERDMAN and GOUGH, 1977; BROWN and BECKETT, 1984). Our present knowledge is restricted more or less to detection of heavy metals, data on the effects of pollutants like SO_2, HF, N-oxydes, etc. (FERRY et al., 1973; TUOMINEN and JAAKKOLA, 1973; FERRY and BADDELEY, 1976; NIEBOER et al., 1978). Although even the occurrence of rare earth metals is reported from some species (ERÄMETSÄ and YLIRUOKANEN, 1971), yet basic information on uptake of essential ions such as Ca^{2+} and K^{+} in undisturbed habitats is still missing (KERSHAW, 1985). This realization led us to using scanning electron microscope-energy dispersive X-ray analysis (SEM-EDXRA)

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to study a wide spectrum of elements simultaneously in different anatomical structures of lichen thalli collected from various environments.

Former bio-indication studies on lichens were carried out within the boundary of Budapest (FARKAS et al., 1985, BORHIDI et al., 1988). This kind of work requests reference material collected from natural, unpolluted environments, thus they were extended to the "Man and Biosphere" (MAB) reservation area located in the Pilis and Visegrádi Mountains (NW from Budapest). Multidisciplinary research carried out in this area aims at indicating the human impact on nature (HORÁNSZKY, 1983).

Hypogymnia physodes (L.) Nyl. commonly occurs all over Hungary. Being relatively tolerant of environmental pollution (it can tolerate up to 90 $\mu g/m^3$ SO_2 in the environment - GILBERT, 1970; HAWKSWORTH and ROSE, 1970; JAMES, 1982) it is the most common foliose lichen even in the moderately polluted suburbs of Budapest (FARKAS, 1982; FARKAS et al., 1985 and FARKAS in BORHIDI et al., 1988) and in the Pilis Mountains (FARKAS, 1988) where samples were collected for the present studies. It is widely used in bio-indication studies in Europe, its morphology, anatomy and ontogeny is under detailed investigation (HALE, 1973, 1976; LŐKÖS, 1983; SCHUSTER, 1985). EDXRA data on lichens are scarce. LAWREY (1977) illustrated the structural localization of accumulated heavy metals (for example Fe) and other elements (Na, Cl, K) in fungal and algal cells of Cladonia cristatella Tuck.; GARTY et al. (1979) studied extracellular deposition of particulate metallic fallout accumulated in Caloplaca aurantia (Pers.) Hellbom. The element composition of particles integrated in the lichen was compared to the element composition of dust particles collected from the surface of the lichen thalli. GARTY et al. (1982) found spores in a lichen-like fossil embedded in Eocene Baltic amber containing mainly iron and sulfur. JONES et al. (1982) - using EDXRA techniques - observed the localization of lead in Stereocaulon vesuvianum Pers. growing on silicaceous limestone.

Materials and Methods

Hypogymnia physodes (L.) Nyl. thalli together with the supporting bark were collected from the sites shown on Fig. 1. These listed according to the increasing degree of pollutedness are the following:

1. P: from Quercus petraea (Mattuschka) Lieblein trunk standing near to the Pilis Peak (757 m) of the Pilis Mountains (21 km NW from Budapest).
2. D: from the trunk of a Quercus petraea (Mattuschka) Lieblein growing at the roadside in the Visegrádi Mountains (23 km NW from Budapest) leading to the Dobogókő, a frequented tourist site.
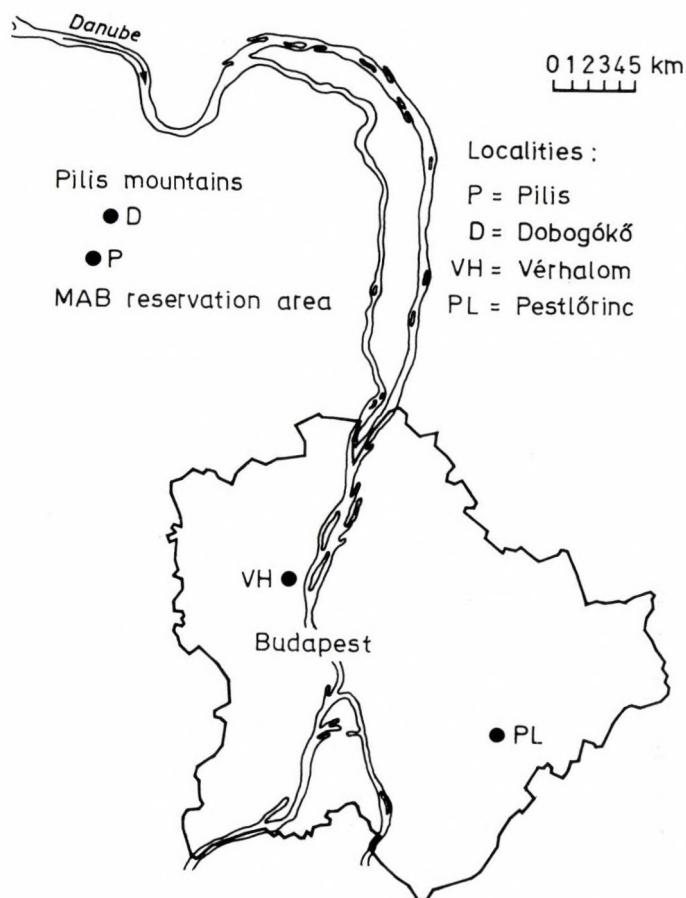
Fig. 1. Map of lichen habitats. Note that abbreviations used on this figure are used throughout in the following

3. VH: from a dying Amygdalus communis L. tree growing in an abandoned orchard at the Buda side of Budapest, in the so-called Vérhalom district.

4. PL: from the trunk of a Robinia pseudoacacia L. tree growing in the abandoned cemetery of Pestlőrinc (SE part of Budapest).

The abbreviations in the legend of the sketch showing morphological structures studied (Fig. 2) were used throughout. For EDXRA studies, about 0.25-0.5 cm^2 pieces of thalli were fixed on stubs using Leit-C Conductive Carbon Cement. The conductive layer was prepared via spraying the specimens with Conducting Film Aerosol (Polaron Ltd., Code No. 0802). Impulses were collected at magnifications ranging from 400x to 700x (3×10^2-10^5 μm^2 areas). The supporting bark, dorsal surface, cross-section of the dorsal cortex, gonidial layer, medulla and ventral cortex were analysed separately. Selecting areas of varying size for analysis is a technical necessity posed by the complicated geometry and texture of lichen thalli at such magnifications. Choosing a representative area calls for circumspection and experience. As mathematical analysis of the data proved, errors attributable to operator subjectivity, in-
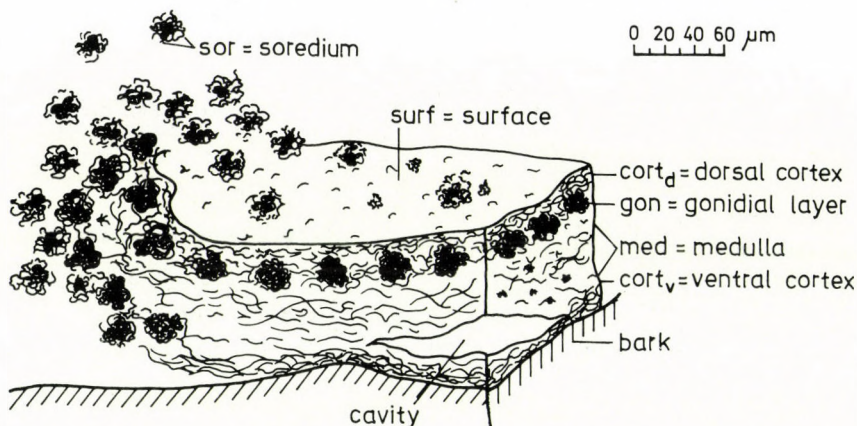
Fig. 2. Sketch of Hypogymnia physodes (L.) Nyl. thallus. Note that abbreviations used on this figure are used throughout in the following

homogenity and heterogenity of the material remained within the limits inherent with samples of biological origin. The EDXRA method is semi-quantitative. In the case of biological samples the energy losses are considerable and the signal/noise ratio is poor. Because of these phenomena and taking into consideration the fact that concentrations of elements change significantly within very short distances in thalli, application of the ZAF correction method is not justified (GOLDSTEIN et al., 1981). Therefore, instead of ZAF, we analysed the raw data using a variety of computer programs. On the basis of these tests we found that the biologically relevant and most informative presentation can be achieved via expressing the concentration of an element as the percentage of the total impulses in the spectrum (corrected for background). Spectra processed in this way then were subjected to statistical analysis using the SYN-TAX package of PODANI (1980, 1988). Program PRINCOMP using correlation of non-transformed data was run for principal component analysis. Euclidean distance based on data standardised by range and complete linkage clustering were calculated by program NCLAS2. Using a makeshift program, rank correlation analysis according to SPEARMAN (SACHS, 1985) was performed.

Results and Discussions

Regarding all samples analysed, we found altogether 16 elements (Na, Mg, Al, Si, P, S, Cl, K, Ca, Ti, V, Fe, Co, Ni, Cu, Zn) present in evaluable concentrations. Considering the elements individually, the following trends were observable.

Concentrations of Na and Mg were always higher in the thalli than in the supporting bark.

Aluminium was found mostly in the barks and on dorsal surfaces of thalli. Within thalli Al is accumulated in gonidia and soredia; the medulla is relatively poor in aluminium.

Silicon was found in very high concentrations in barks and on the dorsal and ventral surfaces of the thalli. In these cases it was clear that

Si is present mainly in mineral particles attached more or less loosely to the lichen thallus surface — although embedded particles are not rare either. Excluding these cases and talking about silicon present in biological structures, i.e. in hyphae and algal cells in non-crystalline compounds, soredia were especially rich in Si.

Aluminium and silicon are regularly present in plants in concentrations comparable to or expressedly higher than the concentrations of common macro-elements. These two elements in biological samples - using exclusively traditional, "wet" analytical methods - can only be measured with difficulties, imprecisely or virtually not at all. Due to this situation data on the biochemistry, importance of these elements in plant life, etc. are scarce. However, SEM-EDXRA routinely detects their presence in plants and, almost automatically, produces information not only on the concentrations but the localization as well. This point deserves more attention than the per se interest of these observations would indicate. Recently an increasing number of papers is published on the conjectured or real toxic effects of aluminium. Not infrequently one can come across opinions declaring certain concentrations of Al toxic while concentrations higher than those by orders of magnitude can regularly be found in normal, healthy plants - with SEM-EDXRA methods.

Phosphorus concentrations were higher in thalli than in the supporting bark without exception. Within thalli the distribution of this element is rather uniform.

Sulfur is slightly concentrated by the thalli in comparison to the substrate. Gonidia and certain regions of medullae may contain amounts significantly higher than amounts present in other structures.

Chlorine occurred in conspicuously high concentrations on dorsal surfaces of thalli in several cases. We consider these occurrences attributable to the particular environments. Potassium was present in thalli in concentrations always higher than concentrations measured in the substrate. The overall concentrations of K in thalli were high and it was especially high in soredia. Calcium seems also to be enriched by thalli. This element is concentrated mostly in the calcified, thick walls of medullary hyphae. Similar situation was found by SAEKI et al. (1977) and by BUCK and BROWN (1979, cit. in Brown, 1987) in Parmelia perlata (Huds.) Vain. where calcium was present bound exclusively to cell walls, in an exchangeable form.

Titanium was present in detectable quantities only in lichen samples from Budapest. In samples originating from the Vérhalom area it oc-

curred in the bark and on the dorsal and ventral surfaces of the thallus. This element occurred in all samples from the Pestlőrinc site, too and in concentrations always higher in the bark than in the thalli.

Vanadium was only detected on the thallus surface of the Vérhalom sample. Titanium and vanadium can often be found together in soil samples during SEM-EDXRA work. Mineral particles containing Ti and/or V can often be found on surfaces of plants. With EDXRA it can also be observed in certain cases that local dissolution of these particles may affect adjacent areas up to distances of several micrometres; however, this phenomenon does not seem to be significant from biological point of view. Concerning the cases under discussion we deem the situation to be the same.

Iron was present in the barks in concentrations higher than in the thalli. Excluding occurrences on dorsal and ventral surfaces, iron is accumulated first of all in structures containing the phycobiont, i.e. in gonidia and in soredia. This observation is in accordance with the findings of LAWREY (1977), who also found the highest concentrations of iron in the phycobiont of Cladonia cristatella Tuck.

Cobalt occurred exclusively in one sample from Pestlőrinc. In this case it was localized in the supporting bark and the ventral surface of the thallus. It clearly originated from the soil of the site.

Ni, Cu and Zn were present in several samples in concentrations near to the limits of detectability. Therefore, data on these elements were excluded from statistical analyses. Microscopical particles of Fe/Ni-containing minerals are common in soils according to SEM-EDXRA studies. They are not uncommonly accompanied with copper and/or zinc. In the present cases we consider these occurrences to be of soil origin, i.e. not results of environmental pollution.

Mathematical analyses of the spectra helped beyond doubt in assessing that to what extent are visually similar spectra close each to other. However, the usefulness of the various methods applied does not seem to be equal. The rank correlation method of Spearman showed correlations between samples originating from the Vérhalom site and, within this group, between the supporting barks and medullae (Fig. 3). Beyond this there were no significant results and the method is not really suitable for processing experimental results of this kind. Cluster analysis (Fig. 4) and principal component analysis (Fig. 5) yielded partially similar results. Spectra of the barks were clearly separated from spectra of the thalli and spectra of identical morphological structures showed high degrees of correlation. (See
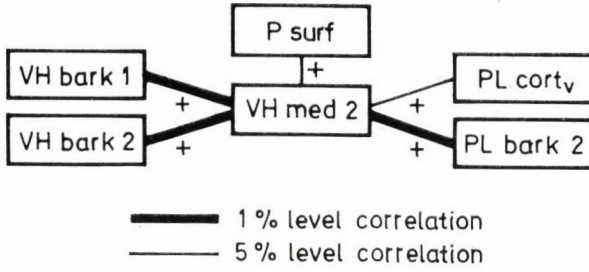
Fig. 3. Spearman's rank correlation analysis of element content data

distance
2.5
2.0
1.5
1.0
0.5

P cort$_v$
P sor
D surf
VH gon 1
VH gon 2
VH cort$_d$
P surf
VH surf
VH cort$_v$ 1
PL gon
PL med
VH bark 1
VH bark 2
PL bark 2
PL bark 1
PL surf-alga
PL cort$_v$
P gon
D gon
VH cort$_v$ 2
P med
VH med 1
VH med 3
VH med 2
P med
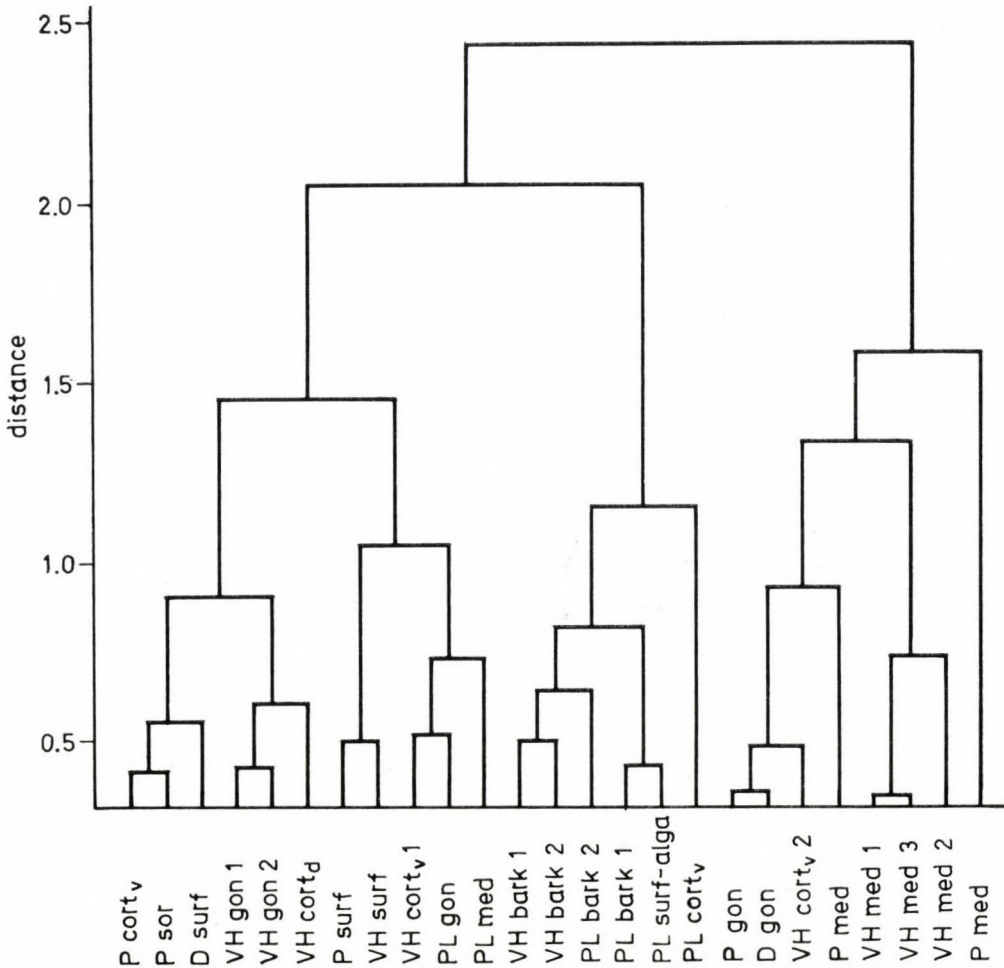
Fig. 4. Classification of anatomical structures of Hypogymnia physodes (L.) Nyl. from four localities
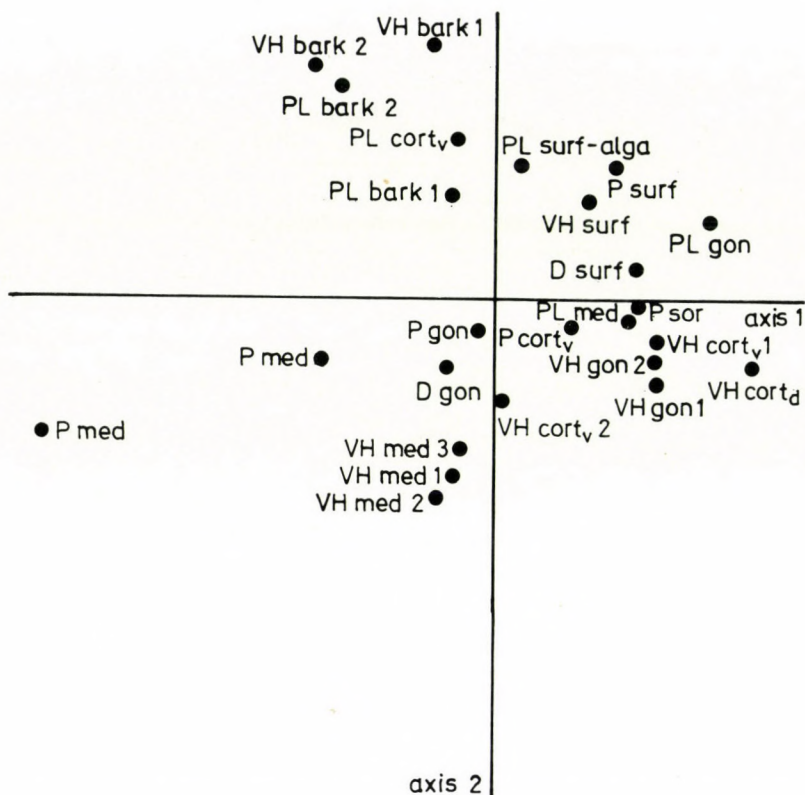
Fig. 5. Principal components ordination of anatomical structures of *Hypogymnia physodes* (L.) Nyl. from four localities: a, scattergram for the 25 objects

the two spectra taken from gonidia or the three spectra characterizing medullae of Vérhalom samples. These examples indicate that subjective, operator errors are acceptable for our present purposes.)

The most interesting and useful results were given by principal components analysis, consequently, this was performed on data grouped according to several different considerations.

Principal components analysis of all the data (Fig. 5a) showed similarities between identical morphological structures of thalli collected at the four different sites (Fig. 5c). Spectra taken from various structures of samples from a given site also proved to be near (Fig. 5b). Similarities were detected between ventral cortexes of thalli and the supporting barks; the same is true for spectra of dorsal cortexes and gonidial layers. To sum up, statistical methods suggest that the primary absorbent
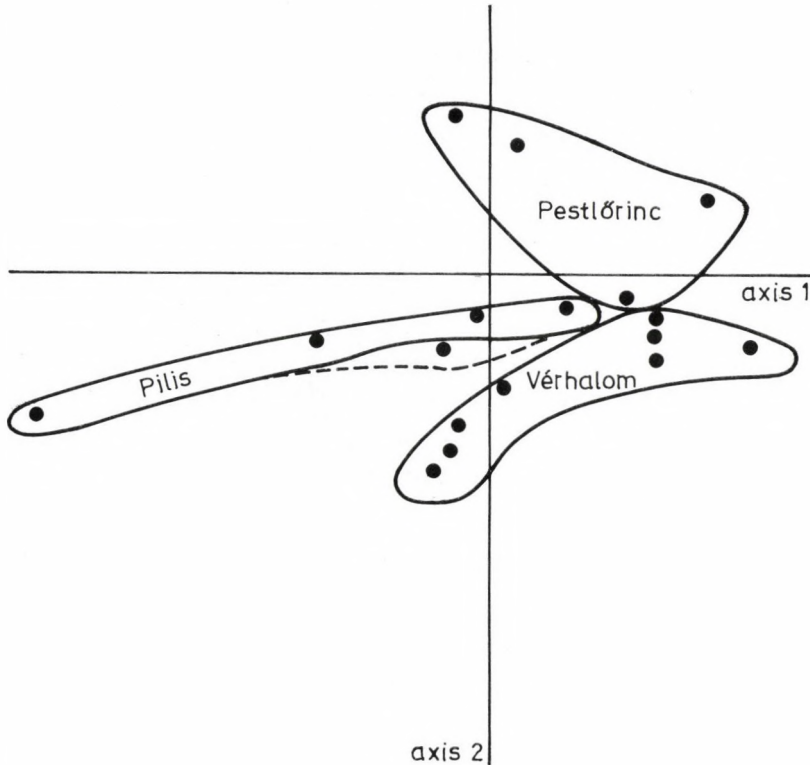
Fig. 5. Principal components ordination of anatomical structures of Hypogymnia physodes (L.) Nyl. from four localities: b, loops engulf objects from the same localities.

is the bark and thalli take up the concentrated materials from there; the chemical composition of the substrate affects the chemism of the thalli. Numerically, the two axes explained 71% of the variance. The first principal component contributed in 31%. The first axis arranges mainly the anatomical structures of the thalli while the second axis arranges mainly the geographical sites. On Fig. 5b separation of spectra according to sites is shown. If spectra of doubtful value (due to particulate contaminations present on surfaces) are excluded then habitats are separated relatively well by principal components analysis. Phanerogamic bark spectra are also well-separated from spectra of the cryptogamic thalli; this is especially clear in the case of spectra of medullae (Fig. 5c). Similarity between the bark and the ventral cortex was only proved in the case of the Pestlőrinc site; the other spectra were arranged along the second axis. Medulla
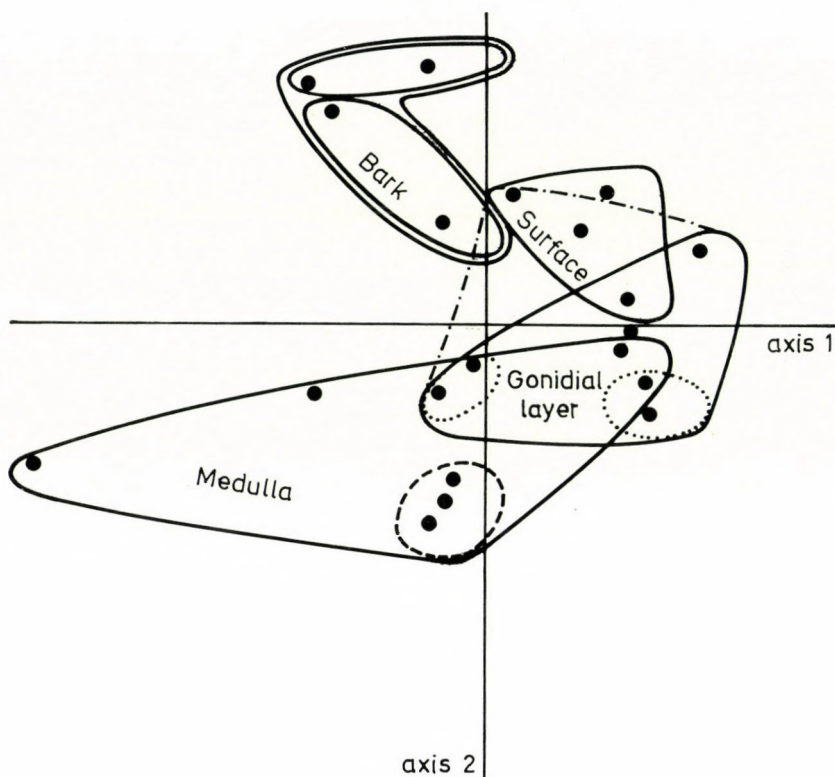
Fig. 5. Principal components ordination of anatomical structures of Hypogymnia physodes (L.) Nyl. from four localities: c, encircled are objects having the same anatomical structures.

spectra — except the Pestlőrinc sample — formed a rather compact group. This behaviour can be explained by the observation that medullary hyphae were definitely thinner and less rich in Ca in the Pestlőrinc sample than in the other cases.

Accumulation of Ca in medullary hyphae can be in correlation with age of thalli and environmental factors as it is suggested by the group formed by principal component analysis from medulla-spectra of the Vérhalom samples. Gonidium-spectra of the thallus from this site are also strongly correlated. One may add these spectra to all the gonidial layer spectra, and in a broader sense, the soredium spectrum of a thallus from a Pilis Peak site because both gonidia and soredia consist of algal cells embedded in fungal hyphae. The thallus surface covered by algae collected at the Pestlőrinc site shows affinity to this group and, at the same time, to spectra
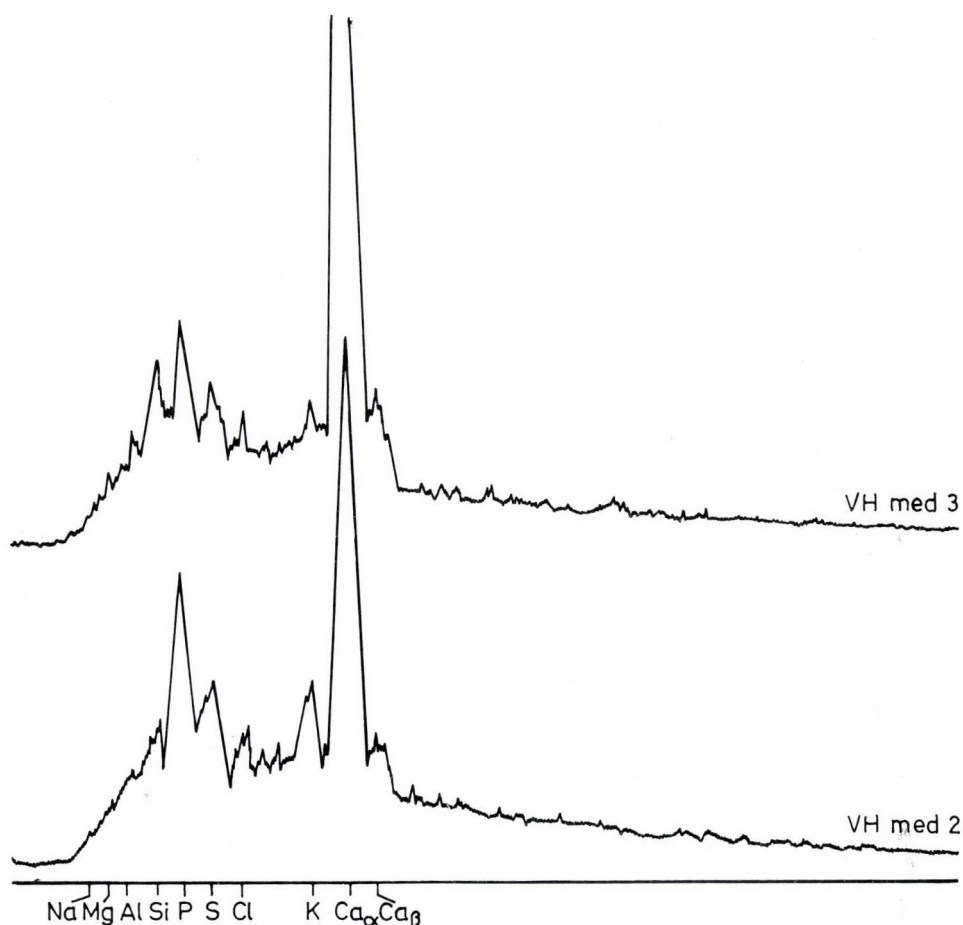
Fig. 6. Two representative EDXRA spectra of Hypogymnia physodes (L.) Nyl. medullae from the Vérhalom site

of thallus surfaces from different sites. The foregoing results are illustrated with representative spectra on Figs 6 (medulla), 7 (gonidial layer) and 8 (bark and ventral cortex).

Analysing the correlations existing between the elements present in reliably measureable concentrations, principal components analysis formed three groups (Fig. 9). Six elements (Na, Mg, S, Cl, K and P) formed a relatively compact group while an another four (Fe, Ti, Si and Al) fell into a somewhat looser one. Ca formed a "group" of its own being separated from all the other elements. This irregular behaviour was studied via running the program on data containing the data of the six-membered group plus
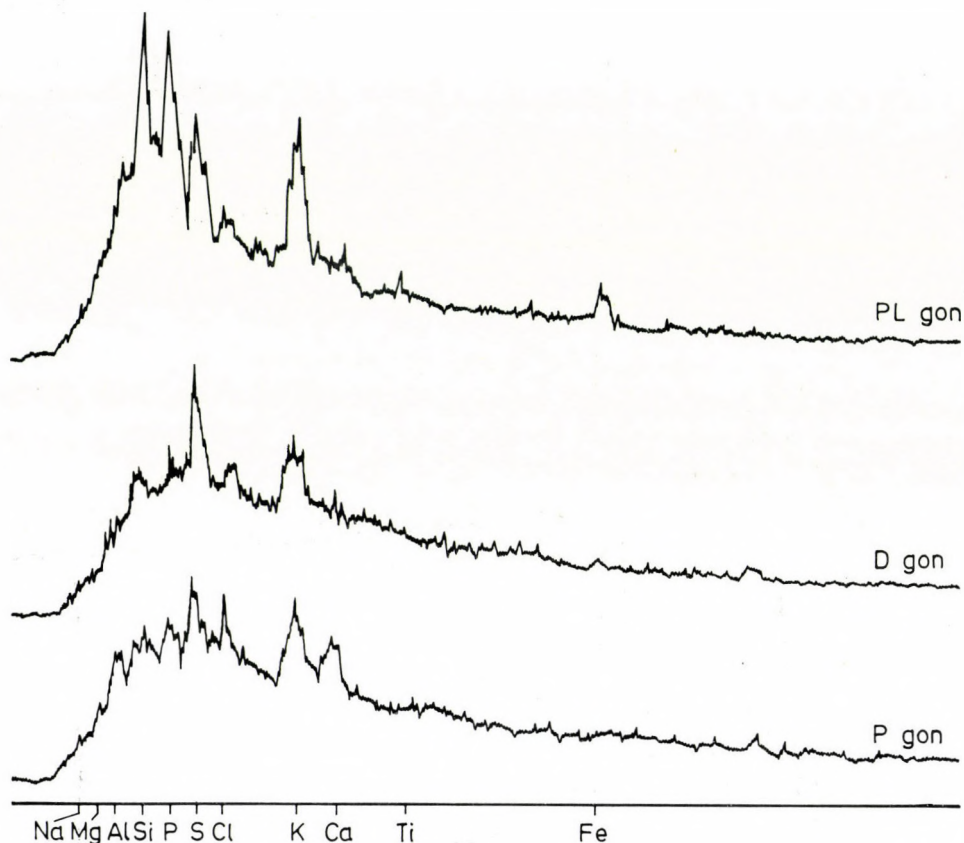
Fig. 7. Representative EDXRA spectra of Hypogymnia physodes (L.) Nyl. gonidial layers from three localities

Ca and on data of the four-membered group plus Ca. The "six-plus-Ca" run yielded a grouping significantly different from the grouping obtained in a "six only" run while groupings of the four remaining elements were hardly influenced by the addition or omission of Ca data. Nevertheless, groups formed during principal component analysis on the data of all the eleven elements remained quite stable in all the versions tried.
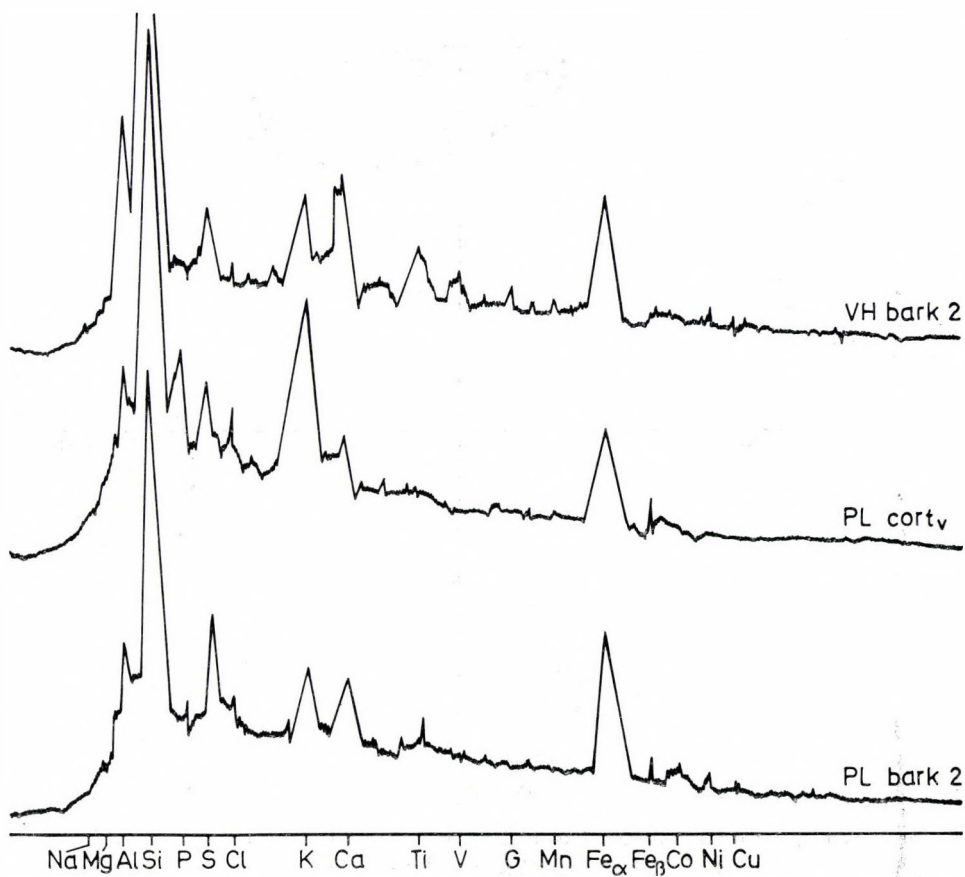
Fig. 8. Representative EDXRA spectra of Hypogymnia physodes (L.) Nyl. ventral cortex and the underlying bark from PL and VH localities
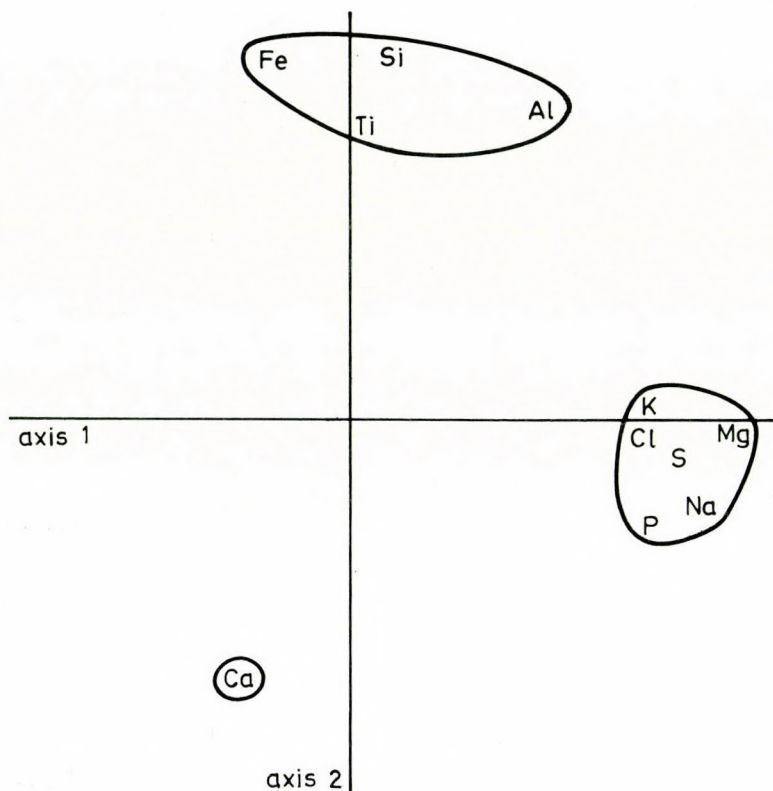
Fig. 9. Principal components ordination of 11 elements according to their concentrations in Hypogymnia physodes (L.) Nyl. thalli

Summary

We found that element compositions of the morphological structures of Hypogymnia physodes (L.) Nyl. thalli are characteristic and can also characterize the habitat in which the lichen grows. As SEM clearly shows, dorsal surfaces of lichen thalli are often heavily contaminated by particulate contaminants of mineral origin. Ventral surfaces are so tightly attached to the substrate that during removal of thalli from substrates they are inescapably contaminated by the substrate - or the removal is non-quantitative, leaving the ventral cortex layer of the thallus more or less behind. Both facts raise doubts about the reliability on data obtained via using digestion of thalli and "wet" analytical methods. On the basis of the SEM picture and principal component analysis of EDXRA spectra, SEM-EDXRA

analysis of the gonidial layers and/or medullae of thalli can be recommended. If one has to choose then the gonidial layer is to be preferred on two counts. This layer is more clearly demarcated and more compact than the medulla. Therefore, errors inherent with EDXRA of biological samples are minimized. From a biological point of view the gonidial layer has the advantage that it contains both the mycobiont and the phycobiont.

Acknowledgements

The authors wish to thank J. Podani and F. Horváth (Institute of Ecology and Botany of the Hungarian Academy of Sciences, Vácrátót) for helping in mathematical treatment of data. The study has been supported by the National Commission of the Technical Development (OMFB) Tt-programme.

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Acta Botanica Hungarica 35(1-4), pp. 73-76 (1989)

FOLIICOLOUS LICHEN-MIMICRY OF A RAINFOREST TREEFROG?+

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(Received: 8 September 1988)

Leptopelis uluguruensis Barbour & Loveridge an endemic Tanzanian treefrog species is recorded from the East Usambara Mountains. Possibility of foliicolous lichen mimicry of this species is discussed and illustrated.

The relationship between lichens and animals is a field where research has seldom been carried out. Our recent knowledge is based mainly on field observations. We know more about lichen-invertebrate associations than about relationships between lichens and vertebrates (for reviews see GERSON and SEAWARD, 1977 and RICHARDSON and YOUNG, 1977).

Lichens are often used as food for certain animals. In other cases lichens serve as a protective environment via concealment (using lichens as shelter), camouflage (wearing whole lichens or pieces of lichen thalli as a mask) or mimicry (the animals' own skins resemble lichens superficially).

Our present observations were made on Leptopelis uluguruensis BARBOUR and LOVERIDGE, an endemic Tanzanian treefrog, during a field trip in the rainforests of the East Usambara Mountains. On November 8th 1986 while collecting foliicolous lichens in a wet lowland rainforest of Amani East Forest Reserve (500 m a.s.l.), our attention was drawn suddenly to a small, pretty greyish-green treefrog (Fig. 1). The greenish white spots and their lichen prothallus-like white margins were the most conspicuous features. We were fascinated by the astonishing resemblance between the frog and sur-

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+Usambara R.F.R. Project publication No. 10.

Fig. 1. Leptopelis uluguruensis Barbour and Loveridge on a Cassipourea gummiflua Tul. leaf (Rhizophoraceae) (about life-size, photographed by T. Pócs)

rounding leaves covered by foliicolous crustose lichens, like Cryptothecia candida, Arthonia, Strigula or Dimerella species (Figs 2, 3).

Fig. 2. Foliicolous lichen thalli which are imitated by the yellowish white or greenish white spots on the dorsum of Leptopelis uluguruensis on a Memecylon erubescens Gilg leaf (about half of the life-size, photographed by E. Farkas)

Fig. 3. We were fascinated by the astonishing resemblance between the frog and the Sorindeia sp leaves covered by foliicolous crustose lichens (about half of the life size, photographed by E. Farkas)

Lichen mimicry is already known amongst amphibians, e.g. Hyla versicolor, the common or grey treefrog of North-America, mimics a piece of bark covered with lichens (WRIGHT and WRIGHT, 1949). RICHARDSON and YOUNG (1977) mentioned that some of the Asiatic horned frogs (Megophrys species) mimic the shapes and colours of leaves and perhaps also foliicolous lichens and algae.

SCHIØTZ's (1975) opinion is that the scattered yellowish white or greenish white spots or small rings placed irregularly on the smooth, wet-looking dorsum of Leptopelis uluguruensis have exactly the appearance of a fungus growing on a wet, decaying leaf.

However, we would like to add that the mimicry may also involve a lichenized fungus growing on living green leaves, as in the specimen we observed. Those specimens which have a brown dorsum with a darker brown pattern more probably mimic fungus on decaying leaves.

We feel that this observation endorses SCHIØTZ's (1975) statement that "These markings... are one of the most striking examples of protective coloration I have seen among African frogs."

Here we would like to express our gratitude to Dr. J. RASMUSSEN (Copenhagen) for the identification of the treefrog. Our sincere thanks also to Antona WAGSTAFF (Österbybruk), Dr. Z. KORSÓS (Budapest), L. LŐKÖS (Budapest), J. MEENKS (Gödöllő) and Dr. L. TIBELL (Uppsala).

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Acta Botanica Hungarica 35(1-4), pp. 77-97 (1989)

COMPARATIVE STUDY OF THE PHYTOMASS PRODUCTION OF MIDDLE- AND EAST EUROPEAN STEPPES

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(Received: 6 January 1989)

The phytomass structure, production dynamics and organic matter turnover were studied in the communities and in dominant and characteristic common species - Festuca rupicola Heuff., Stipa capillata L., Vicia cracca L. and Astragalus onobrychis L. - of Pannonic and Pontic-Ukrainian steppes.

Mass CO_2 fixation of the dominant species and its correlation with environmental factors were also determined.

Introduction

This study is part of the COMECON complex research project entitled "The protection of ecosystems (biogeocoenoses) and landscapes".

The main prupose of our investigation is to discover the plant-soil relations, that determine the nutrient cycles.

The study has two main aspects. The first is the study of water-, mineral- and organic compound cycles at the community level. This includes the study of the structure and dynamics of phytomass, photosynthesis and transpiration. The second is the study of certain soil properties, namely

- dynamics of organic compounds in the soil,
- dynamics of soil moisture and its role in phytomass production,
- dynamics, on different scales, of the composition of soil solution, which has a basic role in nutrient cycles.

This study was carried out in nearly untouched stands of nature preserve areas. So, the results have theoretical value in the study of the structure and function of self-organizing natural systems. On the other hand, they serve contribution to the practice of the maintenance of these stands.

Akadémiai Kiadó, Budapest

The purpose of the recent study is to compare the phytomass structure, production dynamics and ecophysiological behaviour of the common dominant species - Festuca rupicola Heuff. and Stipa capillata L. - in a typical Pannonic steppe relic (Császártöltés, Hungary) and an Eastern European zonal steppe (Chomutovsky Steppe Reservation, Chomutovo, Prae-Azovian region, USSR).

The zonal steppes of the Carpathian basin represent the westernmost part of the Euroasian steppe zone. Regarding climatic conditions, Hungary is a transitional place. In the middle and eastern part of the Hungarian Great Plain forest-steppe represents the zonal vegetation. In this mosaic complex steppe grasslands occur on loess surfaces. Because of the dense human population and the 1.5 thousand-year-old ever-increasing agriculture, the original steppe vegetation has been nearly extinct. Its diverse relic stands can be found on land-slides and at places, where it is very difficult to get to. These refuges have saved lots of typical steppe plants, that are rare in Hungary. So the protection of these areas is an important task. The small dimensions of these steppe patches cause several difficulties in nutrient cycle studies.

Study area

The Pannonic steppe patch studied lies on a sand-loess mosaic near Császártöltés - latitude 46 degree north, longitude 19 degrees east-, in the southern part of Kiskunság, Great Plain, Hungary at an elevation of about 100 meters above sea level. The small relic stand of the Pannonic loess grassland - Salvio-Festucetum rupicolae pannonicum (ZÓLYOMI, 1958) - is situated on a small (200 x 100 meters) loess plateau with steep walls, so it is impossible to cultivate it.

Besides the basin character, the presence of 3 kinds of climatic effects - continental, atlantic and submediterranean - is characteristic of the Hungarian Great Plain. The strength of these effects are different each year. "Continental type" years are the most common, but especially in the distribution of precipitation a submediterranean effect is considerable (BORHIDI, 1961) (see Fig. 1).

The soil of the study area is a thin chernosem with a slight, differentiated profile. Its humus content is little, 2.83% at depth 0-16 cm and 1.27% at depth 16-30 cm. Its texture is sandy loam. According to our survey, this grassland seems to be a floristically rich refuge for both sandy and loess grassland species. The dominant grass species of the closed grassland community are Festuca rupicola Heuff., Chrysopogon gryllus (Torner) Trin., Bothriochloa ischaemum Keng., Stipa capillata L., Poa pratensis ssp. angustifolia (L.) Gaud. The dominance of these species varies with both space and seasons. The most frequent dicotyledons are Astragalus onobrychis L., Medicago falcata L., Seseli varium Trer., Seseli osseum Cr. em. Simk. Besides them Euphorbia pannonica Host, Centaurea sadleriana Janka, Asperula cynanchica L., Pimpinella saxifraga L., Achillea pannonica Scheele and Salvia nemorosa L. are also common. The occurrence of some rare species of Hungarian sandy and loess grasslands such as Astragalus exscapus L. and Taraxacum serotinum (W. et K.) Poir. makes this grassland patch more valuable.

This community has a three-layered vertical structure. The height of the upper layer can exceed 1-1.2 meters (Chrysopogon, Seseli). The second layer (40-60 cm) consists of Stipa
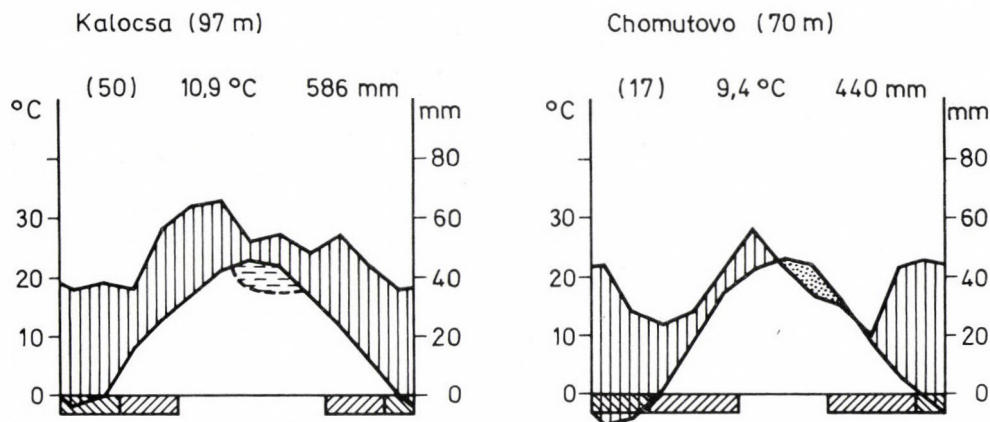
Fig. 1. Climatic diagrams of the areas studied

capillata, Bothriochloa ischaemum, Euphorbia pannonica. The most diverse is the third layer (0-40 cm), where most of the species occur. There is not any moss layer in the community.

In July, when the maximal standing crop occurs, the above-ground phytomass of the Pannonic loess grassland is about 1000-1200 g dry weight/m^2 of which 65% is alive (ENDRÉDI and HORVÁTH, 1976). The underground phytomass in the upper 20 cm is about 1600-1700 g dry weight/m^2, which gives about 60-64% of the total.

The other grassland to be compared is situated in the Chomutovsky Steppe Reservation at village Chomutovo - latitude 46 degrees north, longitude 38 degrees east - 20 km north of the Azovian Sea (Prae-Azovian region).

The slightly wavy loess plateau is deposited on Sarmata limestone. The 1030 ha loess grassland lies at an average elevation of 70 meters above sea level. The climate of the area is continental (see Fig. 1).

Comparing the climate of the two areas some differences can be seen. Both the mean annual temperature and the annual precipitation are higher in Hungary. The seasonal distribution of temperature (Table 1) shows that spring, autumn and especially winter are much milder in the Carpathian basin, where the frostfree period is longer by two months. There are more considerable differences in the amount and distribution of precipitation. The annual course of precipitation is of continental type at Chomutovo. On the other hand, the climate diagram of Kalocsa, which represents the Hungarian study area, shows a typical submediterranean effect - the equinoctial rainfall. This makes the water supply more even, which in turn serves better circumstances for the vegetation. The water supply of plants is reduced at Chomutovo not only by the less precipitation, but by the fact, that at snow melting the winter precipitation can not infiltrate to the frozen soil. Moreover the water of heavy early summer storms can only be poorly utilized because of surface runoff. The summer drought is increased by common easterly wind, that brings dry (30-40 per cent relative humidity) air masses.

The soil of the study area belongs to the temperate, Eastern European facies of typical chernozem. Its depth varies from intermediate to thick, its humus content is relatively little - 3.06% at depth 0-20 cm and 1.96% at depth 40-50 cm. It is slightly or moderately leached. Its texture is clay loam.

According to LAVRENKO's classification (LAVRENKO and KLEOPOV, 1933) the vegetation of the Chomutovsky Steppe Reservation belongs to the drought tolerant version of Ukrainian tall-grass-steppes (Festuca-Stipa-dicotyledons). In this steppe-type the dominant species are Stipa lessingiana Trin. et Rupr., Stipa capillata L. and Festuca sulcata Hack. (F. rupicola Heuff.). To maintain the vegetation, the area is occasionally moved. From this steppe type we tried to choose the community with the most similar species composition and structure to the pannon steppe, for our comparative study. Finally, we chose a Stipa lessingiana dominated stand,

Table 1

Some characteristics of the climatic elements in the study areas

	Chomutovo Ukraine	Kalocsa Hungary
Mean air temperature °C		
winter (12.1.2. months)	-3.4	-0.3
spring (3.4.5. months)	8.8	11.2
summer (6.7.8. months)	22.0	21.1
autumn (9.10.11. months)	9.4	11.2
Yearly average	9.2	10.8
Length of		
vegetation period (days)	215-200	280
frostfree period (days)	200	265-270
Number of days with mean temperature above		
10°C	180	196
15°C	140	142
Precipitation (mm)		
winter	119	114
spring	95	156
summer	134	168
autumn	93	148
Yearly amount	441	586

in which Festuca rupicola, Stipa capillata and Salvia nutans are abundant. So this community is very much like ZÓLYOMI's Salvio-Festucetum rupicolae. It is very rich in species. Besides the dominant species mentioned above Agropyron cristatum (L.) Gärtn., Phlomis tuberosa L., Euphorbia stepposa Zoz., Crambe tataria Sebeők, Ajuga laxmanni (L.) Benth., Stachys recta L. Galium verum L., Stipa ucrainica P. Smirn., Stipa pulcherrima C. Koch and many others occur in this community. This community has also a three-layered vertical structure. The upper layer (above 80 cm) is composed by Stipa capillata, Salvia nutans, Otites chersonensis Kleop., Silene densiflora D'Urv. The middle layer (60-80 cm) is formed by Poa angustifolia (L.) Gaud., Stipa lessingiana, Linum austriacum L., Vicia cracca L.. Festuca rupicola is characteristic of the lower (0-30 cm) layer. There is no moss-lichen layer in this community.

The above-ground phytomass is 600-700 g/m^2 dry matter in June, when the maximum standing crop occurs. The proportion of living parts is only about 50 per cent (BYSTRITZKAYA and OSYCHNIUK, 1975). The amount of underground phytomass is 2700-2900 g/m^2 of which 1800-2100 g/m^2 is concentrated in the upper 20 cm layer. This latter is 75 per cent of the total phytomass.

Methods

To characterize the organic matter cycle, the phytomass structure of model tufts of common dominant species and photosynthetic activity of the same species were compared. To avoid serious destruction of these protected stands, at Császártöltés only 3-3, whereas at

Chomutovo 5-5 model tufts of Festuca rupicola Heuff., Stipa capillata L., Vicia cracca L. and Astragalus onobrychis L. were removed in form of 20x20x15 cm monoliths. The phytomass was separated into living and dead above- and underground parts. The roots were cleaned by washing. The fractions obtained were weighed in air-dry state.

The samples were taken on 07.06.1985 at Chomutovo and on 26.06.1985 at Császártöltés.

Mass CO_2 fixation was measured using the radiocarbon method in the field at the actual temperature, relative air humidity, illumination and wind velocity (ŠESTAK et al., 1971). The glass chamber of the portable instrument was filled with air containing 1 per cent CO_2 with 0.5 mCi/min radioactivity. From grass species three-cm-long pieces were cut from the upper third of the leaves, whereas from the middle part of the compound pinnate leaves of Vicia and Astragalus onobrychis two pairs of leaflets were taken. These pieces were enclosed into the chamber for two minutes immediately after having been cut. After the exposure they were fixed by heat at once. The radioactivity of the samples was determined by Beckman scintillometer in the isotope laboratory of the Eötvös Loránd University. The results are given in terms of fixed CO_2 per dry weight. Measurements were carried out in 5-6 replications. Illumination was measured by a PU 150 type photometer. Chamber atmospheric and leaf surface temperatures were measured by thermometers containing 4MTH type termistors.

Soil moisture content was measured by gravimetry on each day of data collection. Soil samples, each consisting of 3-6 units, were taken from the rhizosphere of the species studied.

Results

Table 2

The phytomass fractions of the model plants
(g dry weight/monolith of 20x20x15 cm)

Chomutovo 7.06.1985.	Festuca rupicola n = 5		Stipa capillata n = 5		Vicia cracca n = 5	
Above-ground living parts	14.2	40.6	16.0	51.1	12.3	22.3
Above-ground dead parts	26.4		35.1		10.0	
Belowground parts	41.1		41.5		35.3	
Total phytomass	81.6		92.6		57.7	

Császártöltés 26.06.1985.	Festuca rupicola n = 3		Stipa capillata n = 3		Astragalus onobrychis n = 3	
Above-ground living parts	14.4	28.9	15.4	31.3	38.4	53.2
Above-ground dead parts	14.5		15.9		14.8	
Belowground parts	52.2		47.5		87.9	
Total phytomass	82.0		78.8		141.0	

Table 3

Mass CO_2 fixation of *Festuca rupicola*, *Stipa capillata*, *Vicia cracca* and *Astragalus onobrychis* in Pannonic and East-European steppe communities

A) CSÁSZÁRTÖLTÉS, HUNGARY

Time		*Festuca rupicola*					*Stipa capillata*					*Astragalus onobrychis*				
		illum.	temperature °C			CO_2	illum.	temperature °C			CO_2	illum.	temperature °C			CO_2
hours	date	Klux	air	chamber	leaf	mg/g/h	Klux	air	chamber	leaf	mg/g/h	Klux	air	chamber	leaf	mg/g/h
	1985.															
	10.05.	50	15.3	19.2	19-22	11.03	60	15.2	19	19-22	12.50	-	-	-	-	-
8	26.06.	64	17	22.8	19-20	6.67	66	16.5	23	19-20	3.61	65	17	22.9	19-20	12.35
	11.07.	36	15.6	19.5	17-18	4.70	40	15.7	19.7	17-18	4.20	42	15.6	20.2	16-18	11.10
	10.05.	75	19.5	22.8	22-24	10.77	76	19.8	24.5	22-24	18.70	-	-	-	-	-
10	26.06.	76	19.2	25.2	22-23	2.71	72	19.2	23.9	22-23	1.39	74	19.6	23.8	21-22	4.04
	11.07.	68	21.6	26.8	26-27	2.90	68	22.3	27.5	26-27	2.80	64	21.6	26.0	25-26	5.30
	10.05.	80	22.5	25.2	-	10.40	80	22	26	-	16.55	-	-	-	-	-
12	26.06.	78	22.2	26	24-25	0.77	78	21.5	26.2	24-25	0.52	74	21.5	25.1	22-24	6.10
	11.07.	56	24.3	27.1	27-28	1.90	54	23.6	28	27-28	0.90	52	24.2	27	24-25	2.80
	10.05.	75	22.2	26	-	13.3	65	22	24.8	-	11.03	-	-	-	-	-
14	26.06.	76	23.2	27	25-26	0.31	74	23	27	25-26	0.10	64	23	25.9	25-26	1.10
	11.07.	22	23.4	25.2	27-28	0.80	20	23.4	24.6	27-28	0.20	16	23.1	24.1	24-25	1.40
16-17	09.05	16	20.8	21.7	-	7.30	19	21	22	-	9.37	-	-	-	-	-
	26.06.	74	24.4	27.5	24-25	0.25	74	24.1	27	24-25	0.06	72	23.8	26.8	23-24	0.72
	9-10.05.			17.70					18.16					-		
Wsoil	26.06.			9.40					8.28					13.14		
%	11.07.			13.90					13.50					16.20		

Permanent wilting percentage = 6%

Table 3 (cont.)

B) CHOMUTOVO, UKRAINE

Time		*Festuca rupicola*					*Stipa capillata*					*Vicia cracca*				
		illum.	temperature °C			CO_2	illum.	temperature °C			CO_2	illum.	temperature °C			CO_2
hours	date	Klux	air	chamber	leaf	mg/g/h	Klux	air	chamber	leaf	mg/g/h	Klux	air	chamber	leaf	mg/g/h
	1985.															
8	04.06.	6-8	17	18.2	-	4.60	11	18	19	-	2.00	16	19	20	-	13.30
	06.06.	60	15	20	-	8.00	56	15	21	-	4.40	64	16.5	22	-	22.20
IO	04.06.	8	18.5	20.1	20-21	1.60	9	18	20	20-21	1.40	8	19	20.1	-	5.60
	06.06.	71	21.5	26	26	4.40	70	21.5	26.2	26-27	3.70	70	22	26.2	-	24.80
12	04.06.	27	21.5	24.9	28-29	7.10	30	21.5	23.9	27-28	4.10	24	22	24.5	-	22.0
	06.06.	78	25.5	27.1	28-30	5.00	78	25.5	27.0	27-28	4.60	78	26	27.1	-	29.6
14	04.06.	66	29	30	29	10.20	22	25	28	24	1.70	28	26	27	-	26.60
	06.06.	80	28	29	31-33	4.00	78	27.5	28.2	28-29	2.20	80	28.5	29.5	-	23.40
17	06.06.	72	25	28.8	28-30	3.80	74	25	29.8	27-28	3.40	70	25	28	-	12.60
Wsoil	04.06.			25.8					26.7							
%	06.06.			16.5					15.2							

Permanent wilting percentage = 9%

Table 2 shows the distribution of phytomass of the model tufts and the proportion of different phytomass fractions. Comparing the amount and structure of the phytomass of the model tufts the following can be stated:
- at the time of sampling, in June, the total phytomass of Festuca rupicola tufts was the same at the two study sites. On the other hand, the total phytomass of Stipa capillata tufts was higher by 15 per cent in the Chomutovsky steppe, than at Császártöltés.

- The amount of photosynthetically active living above-ground parts is surprisingly similar in the same species of the two different steppe communities.

- There is a difference in the amount of underground phytomass of Stipa capillata and Festuca rupicola tufts of the two areas. According to our measurements, in 1985 the weights of underground phytomass of Festuca rupicola and Stipa capillata from Császártöltés are higher by 23 and 13 per cent, respectively, than that of from Chomutovo.

- It is a basic difference, that at Chomutovo the above-ground dead phytomass of both grass species is about twice as much as at Császártöltés. In the Chomutovsky steppe 65-68 per cent of the above-ground phytomass is dead, whereas the same ratio is only 50 per cent at Császártöltés. Earlier studies showed similar or even more serious differences in the phytomass/ unit area data (BYSTRITZKAYA and OSYCHNIUK, 1975; ENDRÉDI and HORVÁTH, 1976).

The distribution of phytomass fractions refers to the differences in the intensity of organic matter turnover of the two steppe communities, which may be the result of different climatic conditions.

The two dicotyledonous species used - Vicia cracca and Astragalus onobrychis - can not be compared on the basis of absolute weight. However, it was observed that the above-ground dead phytomass gives 45 per cent of the total above-ground parts at Chomutovo. At Császártöltés this value is only 28 per cent in the case of Astragalus onobrychis.

Table 3 shows the results and circumstances of CO_2 fixation measurements at the two study areas during five days of data collection.

The photosynthetic activity of the two grass species studied was very similar according to the measurements (Tables 2, 3; Fig. 2) regarding either the daily productivity, or the measured maximal activity. The results of measurements taken to follow seasonal changes can be fitted into one data set. Both species are photosynthetically more active in spring, than in summer, regarding either daily production or maximal activity.

Table 4

Maximum daily intensity (mg CO_2/g.h) and estimated daily amount (mg CO_2/g.day) of CO_2 fixation of Festuca rupicola, Stipa capillata, Vicia cracca and Astragalus onobrychis in Ukraina and in Hungary

Site	Time 1985	Festuca rupicola		Stipa capillata		Vicia cracca		Astragalus onobrychis	
		daily amount	max.	daily amount	max.	daily amount	max.	daily amount	max.
Császártöltés	9-10.05.	132.6	13.3	161.4	18.7				
Chomutovo	4.06.	74.1	10.2	33.0	4.1	210.6	26.6		
Chomutovo	6.06.	60.8	8.0	43.4	4.6	260.6	29.6		
Császártöltés	26.06.	26.9	6.7	14.8	3.6			58.4	12.4
Császártöltés	11.07.	29.1	4.9	26.2	5.6			53.2	11.2
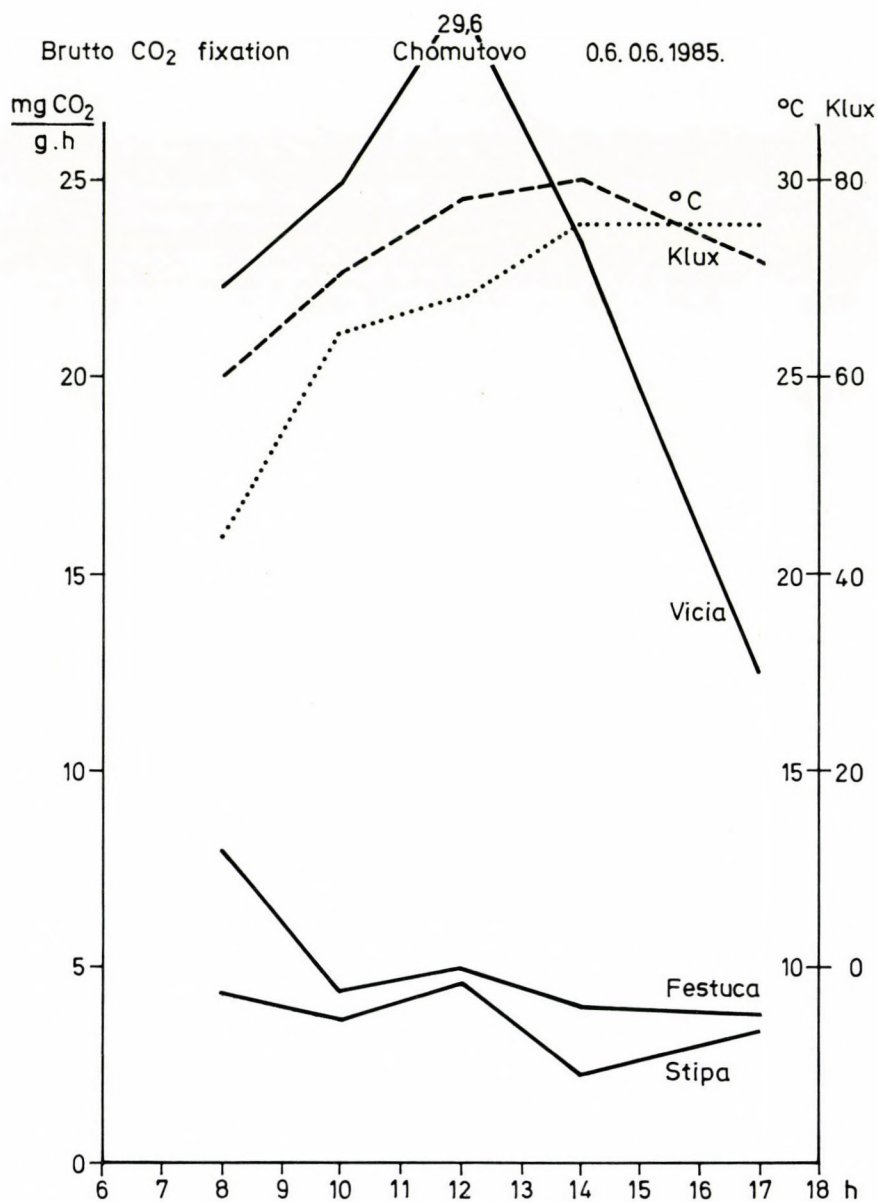
Fig. 2a. Daily course of CO_2 fixation and the actual chamber temperatures and illuminations at Chomutovo
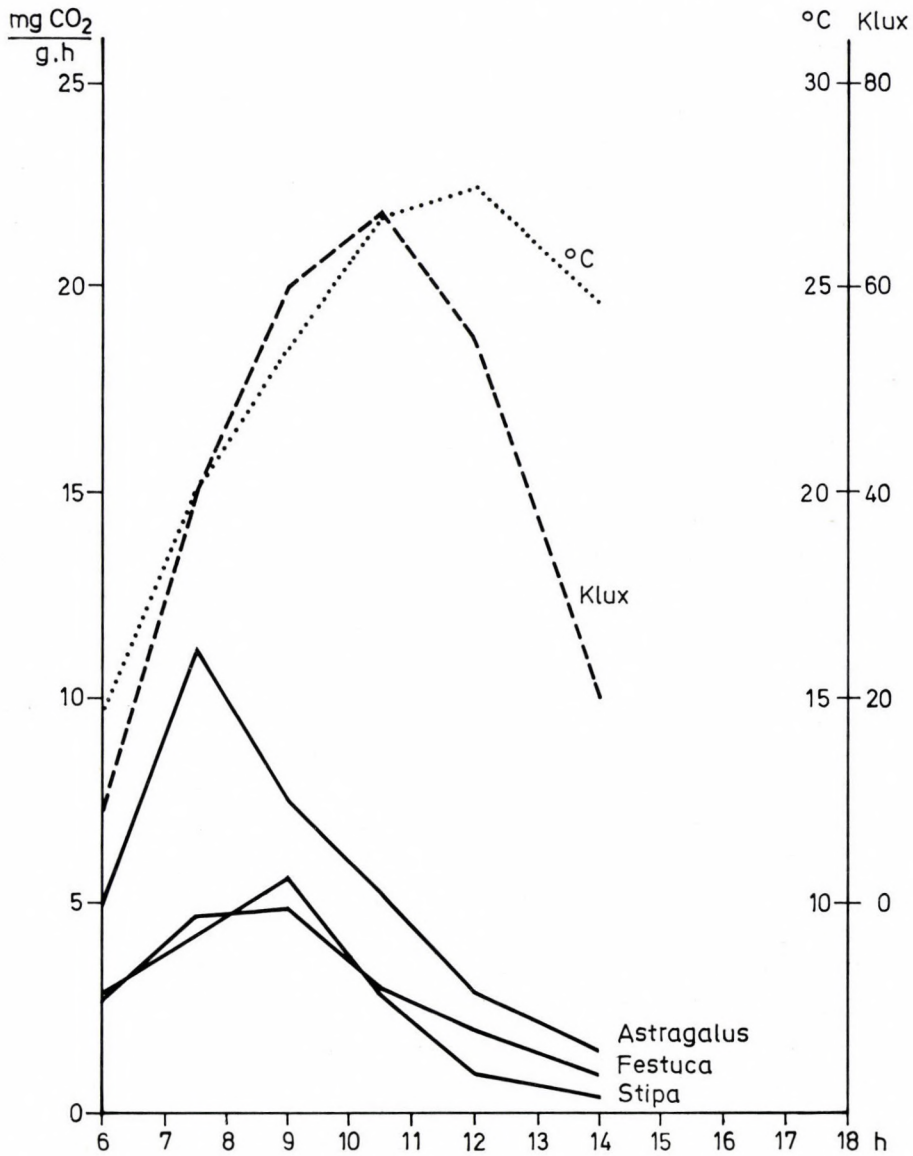
Fig. 2b. Daily course of CO_2 fixation and the actual chamber temperatures and illuminations at Császártöltés

During the investigated period Festuca rupicola usually had higher photosynthetic activity. In May maximal photosynthetic rates of both Stipa capillata and Festuca rupicola were measured around noon. By summer the time of daily maxima of photosynthetic rates were shifted to the morning hours.

On the basis of the daily amount and the time of maximal intensity of photosynthesis the days can be considered as spring or summer types. From the five days of data collection 9-10.05.1985. at Császártöltés were spring type. At Chomutovo 4.06.1985. was rather spring type, whereas 6.06.1985. was rather summer type day (SCHULZE et al., 1975; KOVÁCS-LÁNG and DRASKOVITS, 1985). The two other days (26.06.1985. and 11.07.1985.) at Császártöltés were of summer type.

On spring and summer type days the values and roles of possible influencing environmental factors of photosynthesis are different. This is confirmed by the correlation values in Table 5. In May there is a positive correlation between the daily changes of photosynthetic activity and illumination at Császártöltés in both Festuca rupicola and Stipa capillata. The same was observed at Chomutovo on 4.06.1985. On other days this correlation is much weaker, or it can be negative. This suggests, that photosynthesis is controlled by some environmental factors other than illumination, on these days. The connection between photosynthetic activity and temperature is less direct.

The photosynthetic activity of the two typical steppe species of the pea family always exceeded that of grass species during the period investigated. Vicia cracca showed surprisingly high photosynthetic rate on a summer day (6.06.1985.). On that day Festuca rupicola and Stipa capillata had summer type daily activity (maximal rate at 8 a.m.), whereas Vicia cracca had a spring type day with an around noon maximum.

On summer days the daily course of photosynthetic activity of Astragalus onobrychis is similar to that of grass species. The daily amount of CO_2 fixation of Astragalus onobrychis, on the other hand, is about twice as much as that of the grass species investigated.

Discussion

The amount of accumulating phytomass varies greatly in the continental grasslands of the northern temperate zone. The maximal amount of phytomass in the North American prairie region is estimated as 29 t/ha

(SIMS and COUPLAND, 1979). In Eurasia the following data were obtained: in the grasslands of forest-steppe zone in Kursk Nature Reservation area the total amount of phytomass is about 30 t/ha (SEMENOVA and TIEN-SHANSKAIA, 1966) or 33-38 t/ha (UTECHIN and HOANG-CHUNG, 1976). In Siberia at Baraba it is 28-31 t/ha (BAZILEVICH, 1974), in the steppes of SE-Zabaikal it is 42 t/ha (DRUZHININA, 1973). In the E-Hangai (Mongolia) the maximal amount of phytomass of extracontinental steppes is 39 t/ha (BANNIKOVA et al., 1986).

Earlier studies on the phytomass of the steppe communities studied (BYSTRITZKAYA and OSYCHNIUK, 1975; ENDRÉDI and HORVÁTH, 1976; ENDRÉDI, 1984) show, that the amount of phytomass at the time of maximal standing crop is similar in Hungary and at Chomutovo, 28 and 29 t/ha, respectively. This is in harmony with the similarity of the phytomass of the model tufts collected in the Hungarian and Ukrainian study areas.

There is a great difference within the steppe region concerning the distribution of different phytomass fractions. The more continental the climate, the greater the relative amount of underground parts. According to the available data cited above, the proportion of underground parts of the total phytomass is 60-64 per cent in the Pannonic steppes (Hungary), 70-75 per cent at Kursk, about 75 per cent at Chomutovo (Ukraina), 84-88 per cent at Baraba (Siberia), 83-85 per cent over the Lake Baikal and 87-94 per cent in the E-Hangai (Mongolia). The proportion of underground phytomass ranges from 55 per cent to 81 per cent in the North American prairies. The distribution of above- and underground phytomass of the model tufts studied in 1985 does not satisfy the tendency described above at the community level. The total amount and the proportion of underground parts of both Festuca rupicola and Stipa capillata were higher in the samples taken from Hungary.

To comment this phenomenon there are several things to consider. Earlier studies have shown that the amount of phytomass and the ratio between above- and underground parts can vary with the weather of the year. Comparing the maximal phytomass of the same community at Chomutovo 30-40 per cent differences were found in different years (BYSTRITZKAYA and OSYCHNIUK, 1975).

All samples were taken in the same year, but because of the geographical distance of the two areas, different climatic and weather conditions can be expected.

Another possible question is that whether the sampling process in June refers to the same phenological phase in the steppes or Császártöltés and Chomutovo. At both places Festuca rupicola was in full flower, whereas

Stipa capillata was in a vegetative phase before blooming. In the Hungarian stand the distribution of phytomass of Festuca rupicola and Stipa capillata tufts is similar to that of the whole community (65 and 60 per cent underground parts, respectively). In this respect the Chomutovsky steppe is different. At the community level the underground phytomass is 75 per cent of the total, whereas in June the same ratio for Festuca rupicola and Stipa capillata tufts were 50 and 45 per cent, respectively.

The reason for this difference in the behaviour of these grasses may be the difference in their phenological phases in the two study areas. The total development of Stipa capillata is accomplished by the water deficient period of July and early August at Chomutovo, too. By this time of the year the relative amount of underground parts may be increased.

In spite of the lack of exact data it is assumed, that the root stratification in chernozems might change with the continentality of the climate. So, it is possible that the maximal root mass of Stipa capillata is localized at different depth at the two study areas. SHVYRIAEVA (1971) reported that in similar steppe communities at the Caspian Lowlands the roots of Stipa capillata reach 2.5 meters in depth. On the other hand the maximal root mass was also found in the upper 50 cm of soil.

Another reason for the deviant behaviour of the individuals of the two grasses from that of the community may be the different roles - dominance - of these species in the communities. Festuca rupicola and Stipa capillata are dominant species in the Pannonic steppe stands. The relative importance of them (especially of Stipa capillata) is much less in the much more diverse Pontic-Ukrainian steppes, where the overall root density is much higher as well.

Regarding the ratio of living and dead above-ground parts, the behaviour of the model tufts and the whole community was the same at both localities. In the Chomutovsky steppe the accumulation of dead above-ground parts is considerable. Regarding productivity data which are rather close in the two areas studied (Fig. 3), this may be caused by the slower decomposition.

The turnover rates characterizing the exchange rate of above-ground phytomass (0.65-0.68 in Hungary, 0.44-0.50 at Chomutovo) suggest that the rate of organic matter cycles is less at the more continental Chomutovsky steppe. HARGITAI (1965, 1974) had similar conclusion, comparing the rates of mineralization and humification in the soil. Because of the more intense mineralization, the amount of accumulated humus is much less in the Hun-

April 10 20 30 | May 10 20 30 | June 10 20 30 | July 10 20 30 | August 10

Year	Site	Values (in chronological order)
1967	Ch	6,51 · 3,63 · 4,78 · -0,42 · -4,43 · -2,98
1968	Ch	5,9 · 3,75 · 3,28 · 0,73 · -1,41 · -1,95 · -2,21
1969	Ch	6,07 · 7,57 · 2,39 · -3,05
1970	Ch	7,26 · 9,90 · 1,79 · 3,47 · -4,30
1974	D	6,60 · 6,75 · 6,99 · -10,3 -30.08.
1975	D	1,43 · 4,84 · 6,33 · 6,13 · -5,80 -01.09.
1976	H St.b.	1,46 · 1,97 · -1,06 -05.09.
1976	H St.k.	1,20 · 1,13 · -1,13
1977	H St.b.	1,23 · 0,87 · 1,50 · -1,19 -15.09.
1977	H St.k	1,28 · 1,00 · 1,15 · -1,98

Fig. 3. The productivity of above-ground living phytomass ($g.m^{-2} . day^{-1}$) in the communities of 1. Festuca rupicola + Stipa lessingiana + herbs at Chomutovo (Ch); 2. Festuca rupicola + Stipa capillata + herbs at Dunaföldvár (Hungary) (D); 3. Stipa baicalensis + Carex pediformis + herbs in the Hangai (Mongolia) (H St.b.); 4. Stipa krylovii + Koeleria cristata + + herbs in the Hangai (H St.k.) calculated from data of BYSTRITZKAYA and OSYCHNIUK, 1975; ENDRÉDI and HORVÁTH, 1976; ENDRÉDI, 1984; BANNIKOVA, SUCHOVERKO and BAIASGALAN, 1986

garian chernozems, than in the chernozems of the more continental Ukraina. The average humus content of the chernozems in Hungary is 3 per cent, and it never exceeds 4 per cent. The depth of humus layer rarely exceeds 60-70 cm. In the soils of Ukrainaian steppes the humus layer can be 120 cm, and the humus content exceeds 4 per cent. These facts result mainly from climatic differences. The extremely cold winter and dry summer periods impede microbial mineralization and are favourable for more intense humification.

On the basis of available data it can be stated that rates of daily productivity at the two localities are similar at the beginning of the growing season (April, May), and are much greater, than those of extracontinental steppes in the Eastern-Hangai (Fig. 3). The maximal daily photosynthetic productivity of native North American prairie ranges from 3 to 6.5 g/m^2 depending on climatic conditions (SIMS and COUPLAND, 1979), which is quite close to that of European steppes. However, the period of phytomass accumulation is shorter at the Chomutovsky steppe than in Hungary. Productivity values in Chomutovo always become negative after the end of June, even more in some years after the beginning of June.

It is worth mentioning that the occurrence of maximal daily productivity precedes the optimal (with maximal precipitation) period of the year (Fig. 3) in the Festuca rupicola - Stipa lessingiana - Dicotyledon herbs - grassland community at Chomutovo. It might be the consequence of the soil-moisture reserve, which is available only in spring. In Hungary the increase of phytomass usually lasts until the end of July. The reason for this phenomenon can also be the difference in climatic conditions, which is reflected in the different phytosociological composition and dominance structure of the grasslands of the two areas.

Since the period of phytomass accumulation is longer in Hungary, the amount of organic matter produced is higher than at Chomutovo. In other words the volume of nutrient cycles is higher. In addition to this, the intensity of nutrient cycling is also higher in Hungary.

The measurements were taken during the period of phytomass increase at both localities. The above-ground living phytomass of the model tufts was the same at the two places. It is in good harmony with the intensity of gross photosynthesis of the two grass species. Inspite of the great geographical distance (nearly 1800 km), and different climatic conditions, the diurnal change and intensity of photosynthesis were quite similar at the two areas in both Festuca rupicola and Stipa capillata in the period examined.

Comparing these results with earlier field measurements (KOVÁCS-LÁNG and DRASKOVITS, 1985), it can be concluded, that the daily amount and maximal rate of photosynthesis of xerotherm grasses (Festuca vaginata and Koeleria glauca) of sandy grasslands are on the same scale. Earlier studies concerning the photosynthetic activity of Stipa capillata were carried out in laboratory by GLOSER (1967). GLOSER measured the net photosynthesis of Stipa capillata by IRGA method. Taking dark respiration into consideration he estimated the rate of gross photosynthesis. The results of our summer field measurements are quite close to those estimated values. GLOSER took his measurements at 20 °C, at total water saturation and at a light intensity of about 5-75 Klux. Depending on light intensity the estimated value of gross photosynthetic rate ranges from 2.0 to 4.3 mg CO_2/g dry weight.hour. Our corresponding data range from 1.4 to 4.4 mg CO_2/g dry weight.hour (Table 3).

Having investigated several other Stipa species (S. stenophylla, S. dasyphylla, S. joannis and S. pulcherrima), GLOSER states that the photosynthetic productivity of Stipa capillata is about the half of that of other Stipa species. Since those other Stipa species flower earlier than Stipa capillata, their phenological state at the time of his investigations could be different from that of Stipa capillata. This can be one reason for the differences in the data obtained. According to our results photosynthetic productivity of Stipa capillata varies greatly with its phenological state. In May youngest leaves have high, whereas the summer leaves have much lower photosynthetic activity (Table 4). This decrease can be caused by the enlargement of photosynthetically active surface during the development of the green stem, which increases the photosynthetic productivity of the whole tuft.

GLOSER (1967) investigated the photosynthetic activity of steppe species in relation to the water status of the leaves. According to his results Stipa capillata belongs to the species, that reduce their photosynthetic productivity at relatively little (below 10 per cent) water saturation deficit (WSD). On the other hand at a WSD of 20 per cent Stipa capillata can do 50 per cent of its photosynthetic productivity. Moreover, it works with positive photosynthetic balance at a WSD of 30 per cent. This relation between photosynthesis and water status allows Stipa capillata to complete its development during the dry summer period of steppe region.

Studying water retention capacity of steppe plants, KVĚT and RYCHNOVSKÁ (1965) grouped Stipa capillata and Festuca rupicola to the xeric

Table 5

Correlations between the daily course of CO_2 fixation and illumination and temperature in the exposure chamber

x_1 = illumination; x_2 = temperature

	r_{yx_1}	r_{yx_2}
Császártöltés 9-10.5.		
Festuca rupicola	0.73 ± 0.34	0.52 ± 0.43
Stipa capillata	0.68 ± 0.37	0.32 ± 0.47
Chomutovo 4.6.		
Festuca rupicola	0.88 ± 0.34	0.86 ± 0.36
Stipa capillata	0.82 ± 0.40	0.17 ± 0.70
Vicia cracca	1.00 ± 0.0	0.95 ± 0.22
Chomutovo 6.6		
Festuca rupicola	- 0.82 ± 0.33	- 0.97 ± 0.14
Stipa capillata	- 0.43 ± 0.52	- 0.96 ± 0.16
Vicia cracca	0.45 ± 0.52	- 0.12 ± 0.57
Császártöltés 26.6.		
Festuca rupicola	- 0.89 ± 0.26	- 0.99 ± 0.08
Stipa capillata	- 0.88 ± 0.27	- 0.90 ± 0.25
Astragalus onobrychis	- 0.23 ± 0.56	- 0.83 ± 0.32
Császártöltés 11.7.		
Festuca rupicola	0.30 ± 0.48	- 0.32 ± 0.47
Stipa capillata	0.44 ± 0.45	- 0.33 ± 0.47
Astragalus onobrychis	0.36 ± 0.47	- 0.32 ± 0.47

grasses. On the other hand they stated that in these two species the water retention capacity of the leaves varies greatly, depending on the habitat. This refers to good adaptive properties of these species, which allows them to occur in different communities and a wide geographical distribution.

The gross photosynthetic rates of the two selected species of the pea family (*Vicia cracca* and *Astragalus onobrychis*) are 2-3 times as a high as that of grass species. The same ratio was found between the Astragalus and grass species of the extracontinental steppes in the Hangai (Mongolia) (SLEMNIEV and BOLD, 1983).

During the growing season photosynthesis is limited by different environmental factors. In spring it is controlled by illumination (c.f. corresponding correlation coefficients in Table 5). By summer this light control disappears. Comparing the correlation coefficients with the corresponding data of soil moisture (Table 3) it is obvious, that light limits photosynthesis only at high soil moisture contents, i.e. the plants have sufficient water supply (9-10.05. Császártöltés, 4.06. Chomutovo). Az intermediate water supply (6.06. Chomutovo, 11.07. Császártöltés) the correlation between light intensity and photosynthesis is much weaker. Below a threshold in soil moisture content water becomes the limiting factor of photosynthesis. Similar behaviour is assumed in the plants of the steppes in the E. Hangai (Mongolia) (SLEMNIEV, 1986).

Summary

Comparing the phytomass structure, production dynamics, phytomass turnover and the ecophysiological behaviour of the common dominant grass species - *Festuca rupicola* Heuff., *Stipa capillata* L. - and that of two dicotyledonous species - *Vicia cracca* L. and *Astragalus onobrychis* L. - in a Pannonic steppe relic (Császártöltés, Hungary) and in an Eastern European zonal steppe (Chomutovsky Steppe Reservation, Prae-Azovian region, USSR) the following can be stated:

- The total phytomass of *Festuca rupicola* tufts was the same at the two study sites, whereas that of *Stipa capillata* tufts was higher by 15 per cent in the Chomutovsky steppe.

- The amount of above-ground living parts is similar in the same species of the two different steppe communities. It corresponds with the similar gross photosynthetic activity measured of the two grass species.

- In the Chomutovsky steppe the amount of the above-ground dead phytomass of both grass species and the dycotiledons is about twice as much as at Császártöltés, Hungary. This refers to the differences in the intensity of organic matter turnover of the two steppe communities, mainly to the faster decomposition processes in Hungary.

- The amount and proportion of underground phytomass of both Festuca rupicola and Stipa capillata was higher in the samples taken from Hungary. It does not fit to the tendency determined by climatic conditions.

- The photosynthetic activity of the grass species was very similar regarding either the daily productivity or the maximal daily activity. Daily and seasonal changes in the course of gross photosynthesis could be detected. The maximal activities measured at noon on spring days decreased and were shifted to the morning hours in summer days.

- The influence of environmental factors on photosynthetic activity changed during the vegetation season. Under optimal soil moisture conditions illumination limited gross photosynthesis, while during dry summer period lack of water was the main limiting factor.

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Acta Botanica Hungarica 35(1-4), pp. 99-125 (1989)

AN EXPERIMENTAL APPROACH TO THE STUDY OF COMMUNITY STABILITY: RESILIENCE AND RESISTENCE

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(Received: 18 October 1988)

The relative ecological stability of an old perennial grassland community was studied by selective removal of dominant and subordinate species. Community resilience after disturbance and resistance against drought were assessed by comparing control and herbicide-disturbed plots with respect to total cover, species richness (S), diversity (H) and evenness (E), over 9 years. Annual changes in dominance structure, dominance-diversity curves and rank order of species were also followed.

The changes of total cover, S, H and E values were not sufficiently informative to assess resilience. The simultaneous changes of the two diversity components (S, E), however, were good indicators of resilience and resistance behaviour. The distribution of the relative abundance of species was unsuitable to indicate resilience, and the effects of disturbance and climatic perturbation. Community resilience during the localized succession, implying mainly the existence of a shifting pattern of relative abundances, could be best described by the rank order changes of some important species. The pattern of dominance sequence of dicots and monocots seemed to be the best indicator of restoring the original "structure" and "function".

It was clear that in the assessment of community stability biological properties of populations and autecological features of species may be more important than statistical community attributes, such as H and S. The study of the response of particular species through time was also necessary for an appropriate interpretation of the results on community stability. Owing to the different life history strategies and adaptive properties of monocots and dicots, there were great differences, mainly in the response to disturbance, over time. Although the manner and degree of the changes were entirely different at every treatment, the similar direction of changes, and the tendency of recovery became evident during the investigated period. The differently disturbed community could return to its predisturbed state nearly after 9 years. (The *Pulsatillo-Festucetum rupicolae* community existed in elasticity (WESTMAN, 1978) of 9 years.)

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Introduction

One of the most important problems in contemporary ecology is the change of stability during secondary succession and the relationship between stability and other community characteristics. However, there is a great confusion and contradiction in the ecological literature with respect to the concept of stability and its relationship to community structure and function. This problem generated much speculation and relatively little experimentation, although it is obvious that empirical data are needed to determine stability relations in different communities.

In this paper relative ecological stability (SMEDES and HURD, 1981) of an old perennial grassland community is tested by controlled disturbance experiments. Selective species-group removal techniques have been applied to examine some aspects of community stability and some features that affect it.

In this study, two ecologically important aspects of stability are distinguished (HARRISON, 1979; REJMANEK, 1979);

1) resistance: the ability of a system to avoid displacement during the stress period after external perturbation (= resistance against drought);

2) resilience: the ability of a system to approach a previous state following disturbance (HOLLING, 1973; ORIANS, 1975; HILL, 1975; HARRISON, 1976, 1979). Disturbance in my experiments was defined as a herbicide agent that caused changes in the community state. As a general ecological definition, the term resilience refers to the pace, manner and degree of recovery of the community properties following human disturbance (WESTMAN, 1978, 1985, 1986; REJMANEK, 1979; LEPŠ et al., 1982; KINDLMANN and LEPŠ, 1985).

Major floristic changes and relative ecological stability relations of the community studied have been reported earlier (VIRÁGH, 1987a). In that paper I analyzed the effect of treatments on the coenological similarity relations, the direction of secondary succession, the rates of change measured in terms of floristic and cover change (BORNKAMM, 1981, ARMESTO and PICKETT, 1986), the degree of the seasonal dynamics and the responses to stress situation (resistance). Then, vegetation pattern and major trends of temporal floristic changes were also examined by multivariate methods (VIRÁGH, 1986, 1987b). It was concluded that the results of floristic similarity analyses and ordinations are quite good indicators of resilience.

In this paper the effects of selective removal of dominant and subordinate species from the community and changes of the dominance structure in 9 years are examined. The pattern of change in the total cover of vegetation, species richness and diversity is used to assess the resilience of the old perennial grassland community and its response to stress situation (resistance against drought).

The study aims to answer the following questions:

- Can we predict relative ecological stability relations of a community from its synphenomorphological and coenological features?
- Are species richness, diversity and the distribution of relative abundances indicative of community resilience?
- Besides the floristic composition, which community characteristics would be sensitive indicators of resilience?
- How does the degree of resilience vary with the community attributes measured?
- What is the effect of selective removal of dominant and subordinate species on the resistance of the community to drought and on the degree of resilience after disturbance?

Material and Method

Field experiment

The study area is located at the southern foot of the Bükk Mountain (NE Hungary), about 200-300 m above sea level. The vegetation is a secondary steppe community: Pulsatillo-Festucetum rupicolae (MÁTHÉ and KOVÁCS, 1962), near stable state. A detailed description of this community is given in VIRÁGH (1982) and VIRÁGH and FEKETE (1984).

The research program was launched in 1979 in a homogeneous stand of the Pulsatillo-Festucetum rupicolae and the experiments ran for 5-9 years. The main purposes of this study, the types of experiments and the herbicides applied are described in detail by VIRÁGH (1982, 1986, 1987a).

This paper considers the selective removal of monocots and dicots from the sward for studying structural changes and regenerational processes. Five types of experiments were carried out, there are:

Control (without any treatment)

It represents structural and population dynamical changes of the intact original community.

Treatments with Gabonil (MCPA + dicamba = 4-chloro-2 methyl-phenoxy-acetic acid + 2-methoxy-3,6-dichlorobenzoic acid)

Doses applied were 4 l/ha and 7 l/ha.

All the dicots, the less dominant constituent species, were removed.

Treatments with Dalapon (2,2-dichloropropionic acid)

Doses applied were 12 kg/ha and 20 kg/ha.

The dominant monocots were removed.

Sampling

The experiments were arranged in a randomized block design with 5 replications per treatment. The detailed investigations were carried out in 1x1 m^2 permanent quadrats covered with a grid of 20x20 cm^2 units (see VIRÁGH, 1982).

Presence-absence and percentage cover of each species, visually estimated, were recorded in a set of contagious subquadrats (125 in total per treatment).

The area was sprayed (at one occasion) at the end of June 1979, except for the two selective herbicides of larger dose which were repeated again after a year.

Floristic composition of treated quadrats was recorded before and after the treatments in June and in September from 1979 to 1983 and then in 1987. The control plots were also examined twice a year.

Data

In the previous publications the results of similarity analyses were based on the presence/absence and cover data for each species in the 20x20 cm^2 subquadrats. The five 1x1 m^2 quadrats are now considered as single "operational" unit, but variation between the 5 replicate plots is not shown. In order to follow the structural changes during the 9 years, the percentage cover of each species was summed over for all the quadrats of each individual treatment. Thus, the analyses were made at the level of experiments rather than quadrats. The initial condition of all treatments was similar, so differences in community structure of the treatments can be attributed mainly to the effects of herbicide spraying. I focused on the temporal changes of structural characteristics of each treatment separately and interpreted the differences between control and treated experiments.

Methods used

On the basis of total cover data of every species, several measures of community structure were calculated for each experiment. These were the following:

1) total cover of the vegetation,
2) relative ratio of monocots to dicots,
3) species richness,
4) species diversity and evenness,
5) dominance-diversity curves and
6) constancy of relative cover of species.

Species richness is the total number of species for each date of sampling in each experiment. Species diversity was calculated as: $H' = -\sum \hat{p}_i \ln \hat{p}_i$ (SHANNON, 1948), where $\hat{p}_i$ is the relative cover of species "i". The evenness measure used here is based on this diversity index and is defined as:

$$E = \frac{H' - H'_{min}}{H'_{max} - H'_{min}},$$

(HURLBERT, 1971), where $H'_{max} = \ln S$, S is the total number of species and $H'_{min} = \ln(N)-(N-S+1)$, N is the total cover of species. Nonparametric statistics were used for all comparisons of community structure. The Wilcoxon matched-pairs signed-ranks test (SIEGEL, 1956; SOKAL-ROHLF, 1969) was applied to determine if significant differences occurred in total number and cover values of species, as well as H and E values between control and treated experiments over a 9 year period of time.

In order to draw the dominance-diversity curves the relative cover of each species, as a measure of species importance, was calculated. Curves were constructed also from each species x time matrix referring to the treatments separately.

To describe community resilience the changes of relative abundance of some particular species were also followed from year to year during the secondary successions.

Results and Discussion

1. Vegetation cover and relative proportion of monocots and dicots

Nine year change of total vegetation cover in the control and treated experiments is presented in Fig. 1. Spring and summer precipitation during the period from 1979 to 1987 is also illustrated to examine the effects of wet and dry seasons on total cover values. Figure 2 showing the relative percentage proportion of monocots and dicots with time provides some insight into the observed differences in total vegetation cover.

Control experiment

Total cover in the intact community fluctuates during the 9 years, showing mainly the effects of seasonality and the climatic differences between years. The high cover in September 1979 is probably due to the great expansion of *Bothriochloa ischaemum* and some other species (*Luzula campestris*, *Leontodon hispidus*, *Thymus marschallianus*, *Potentilla arenaria*, *Genista tinctoria*). This unusually high abundance in autumn is probably in response to the even and relatively high rainfall of that year. In the subsequent two years when the total precipitation of the growing season is high above the 50 years mean, the vegetation cover remains at high values. There is a great decrease in the autumn of 1982 in response to the extreme dry summer. Similar declining tendency is typical for the year of 1983 and also for 1987 due to the subsequent extreme dry summer periods. (Total cover is the only attribute in the control that strongly indicates the effect of drought.)

The monocots account for 40-50% of the total cover in the control. This proportion between monocots and dicots is about the same during the investigated period (indicating only the effects of seasonality).

Gabonil experiments

In the *Gabonil 4* experiment, the treatment has caused significant decreases in percentage cover of dicots. Relative proportion of the monocots immediately after herbicide spraying becomes 2.5 times higher than before the treatment. Reinvasion of dicots is very slow due to the great expansion of monocots, as well as strong competition and K-strategy behaviour of the perennial grasses. Five years after the treatment, the community can be still characterized by the predominance of monocots. The proportion

of monocots and dicots reaches the predisturbed, original state only by the 9th year following the spraying.

The herbicide treatment has also caused a decrease in the total cover of vegetation. Since by the autumn of 1979 the total vegetation cover in the control experiment increased by 43%, in this experiment the deviation from it can be considered as being about 48% (see Fig. 1). This is the effect on total cover, for which the Gabonil herbicide with smaller dose must be exclusively responsible. Naturally, in this case we supposed that in the homogeneous stand of the community vegetational dynamic processes of similar extent and direction would have happened in all plots before the disturbance. After the decrease induced by the herbicide effect, there is a strong subsequent increase in the total cover, but in spite of this, the cover values always remain significantly smaller than those in the control experiment. One year and half after the spraying the cover changes show fluctuation caused by more and more re-appearing dicots and a decreasing trend similar to control. The effects of the severe drought in 1982 and 1987 on the total cover are about the same compared with the control plots, indicating similar response of the vegetation to external (climatic) perturbation. All these show that the behaviour of the coenostates after disturbance by Gabonil herbicide is mainly determined by the dominant monocots, like in the intact community. It must be also noted that though the resistance to stress situation is similar in the control and the Gabonil experiments, the recovery after the drought period is much slower in the treated plots than in the control ones (Fig. 1). It also means that the coenostates of the plots characterized by the pre-dominance of monocots can regenerate slowly (small "resilience" of the disturbed "community").

Larger dose of Gabonil 7 brought about much more significant deviations than the lower dose. The repeated spraying in 1980 killed the dicots almost entirely. Reinvasion by these species was restricted and germination of their seeds was also inhibited (see VIRÁGH and GERENCSÉR, 1988) for a long time. The monocots still accounted for 85-95% of the total percentage cover by the end of 1983. This value is 200-250% higher than in the intact community indicating complete disintegration of cover-abundance relations. Such drastic changes might suggest that recovery is completely impossible. However, in a relatively short time, during the subsequent 3 and 4 years, population and vegetation dynamic processes resulted in gross changes toward returning to the original state. After predominance of monocots lasting for about 5 years following disturbance, by 1987 the proportion of mono-
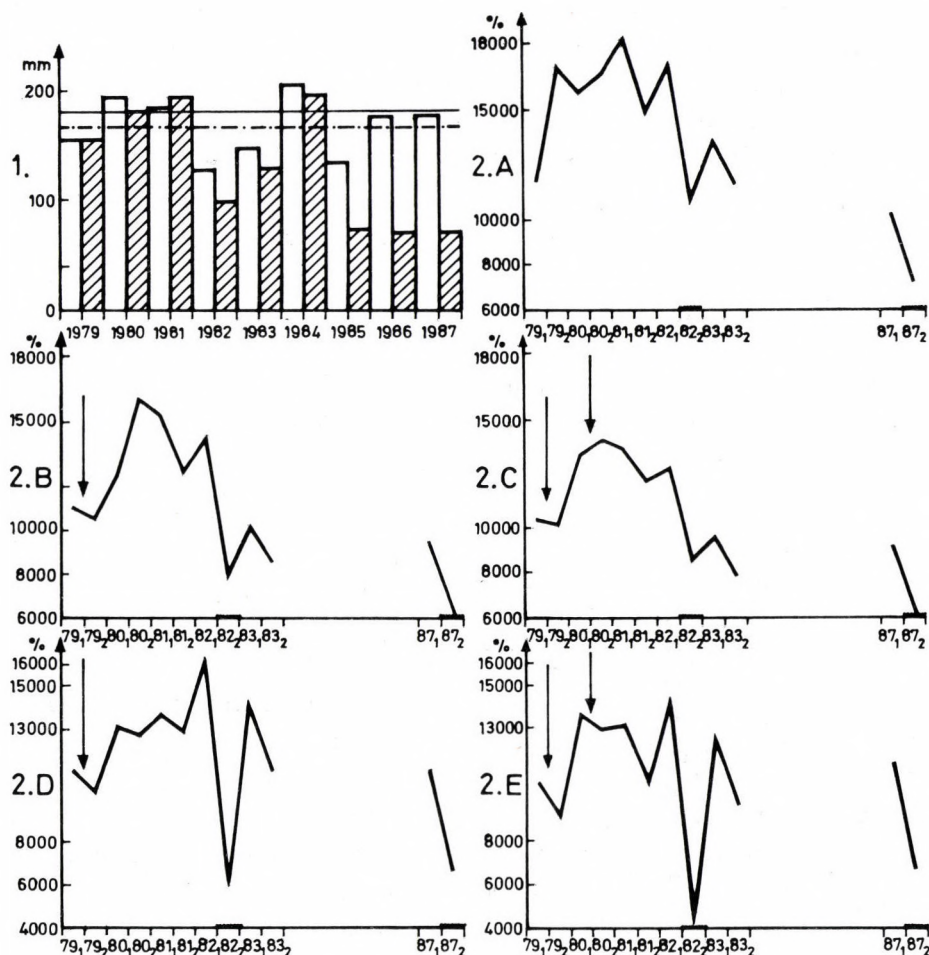
Fig. 1. 1) Spring ( ) and summer ( ) precipitation from 1979 to 1987 and the effect of drought summers on the total vegetation cover. 2) Changes of total vegetation cover. - A: Control; B: Gabonil 4; C: Gabonil 7; D: Dalapon 12; E: Dalapon 20; - 79_1: June 1979; 79_2: Sept. 1979; 80_1: June 1980; 80_2: Sept. 1980; 81_1: June 1981; 81_2: Sept. 1981; 82_1: June 1982; 82_2: Sept. 1982; 83_1: June 1983; 83_2: Sept. 1983; 87_1: June 1987; 87_2: Sept. 1987; Arrows indicate date of spraying by herbicide; Dotted lines indicate drought periods

cots and dicots became similar to that in the pre-disturbed and control community. At that time there was no difference between the different Gabonil doses either.

In the course of 9 years the tendency in total cover changes shows high similarities in the Gabonil experiments. In case of larger dose, however, because of the doubled effect, the increase in cover is much smaller than in the lower dose. Furthermore, due to the absence of many dicots the drought of 1982 has also less impact on the total cover changes. Magnitude of response to drought in cover changes differs by 10% from that in the Gabonil 4 and control plots. In 1987, when the community approximately regained most of its pre-disturbed state with similar floristic composition, the decrease in total cover in response to drought is about the same compared with the control and the Gabonil 4 experiments.

Dalapon experiments

In the Dalapon experiments predominance of dicots was remarkable throughout the first 5 years following disturbance. It was very important that after eliminating the dominant monocots large bare ground occurred where some dicots well, spreading by vegetative propagula became predominant and determined subsequent changes. The monocots re-appeared only 2-3 years later. Nevertheless, still in 1983, the monocots had a share in the total cover only with about 18%. This relative percentage cover value is 54% lower than in the original intact state in 1979. At the same time, 5 years after the first disturbance, the proportion of monocots in case of larger dose is much smaller compared with that in the lower dose. It indicates slower recovery with high level of repeated disturbance. In the 9th year of dose, the proportion of monocots and dicots approximates but has not reached completely the percentage typical for the pre-disturbed state. It can be supposed that the Dalapon-treated plots require the longest time for their recovery.

The effects of herbicide can be well seen in the strong change of total cover. Removal of the dominant species caused much larger decrease in cover related to the effects of Gabonil herbicide. Then the gradual increase in cover and its rather great fluctuation due to the dicots are very similar to the control. There is, however, a marked difference in the level of increase in cover. In 1982 the total cover decreased drastically in response to drought. The cover change is 60-70% indicating 20-30% larger decrease than in the control and Gabonil experiments. The reason of this pro-

nounced cover loss may be the disappearance of individuals of many dicot and monocot species, as well as the strong decrease in vegetative cover of certain plants (Hieracium pilosella, Leontodon hispidus, Potentilla arenaria, Plantago lanceolata and Luzula campestris) altogether with the persisting drought. The Dalapon-treated plots characterized mainly by dicots proved to be very sensitive to drought. This high level of herbicide dose makes the vegetation more susceptible to this climatic risk. In 1983 the total cover is very high again. It can be stated that on the basis of relations to stress situation, these coenostates are slightly resistant, but because of the dominant dicots with their flexible responses they can regenerate. Thus, in the respect of total cover changes the resilience of these coenostates is unambiguous. The vegetation cover in the summer of 1987 is about the same, or little higher related to that in the control at that time and in the predisturbed initial state. Although the total cover returned to the control situation, the species composition remained different (see Fig. 2) suggesting different ecological implication of the same cover values and similar changes. The cover decrease being 10% stronger than in the intact community after summer drought of 1987 also demonstrates that the community with many dicots may be more unstable and sensitive against the climatic perturbation compared with the control and Gabonil-treated community.

Table 1

The results of WILCOXON's signed-ranks test for two groups, arranged as paired observations

Total vegetation cover of two experiments, compared over "9 years" (n=12 sampling points of time)

	Control-Gab.4	Control-Gab.7	Control-Dal.12	Control-Dal.20	Gab.4 - Gab.7	Dal.12 - Dal.20
T_s	0	0	9	1	12	8
P	>0.10% xxx	>0.10% xxx	1% xx	>0.10% xxx	2% x	0.5% xxx

The result of Wilcoxons' test for paired comparisons is reported in Table 1. Comparison of the annual summer and autumn total cover for control and treated plots over 9 years shows that there is a statistically significant difference between control and every disturbed experiment. There is only a slight significant difference between the treatment with lower and larger dose of Gabonil.
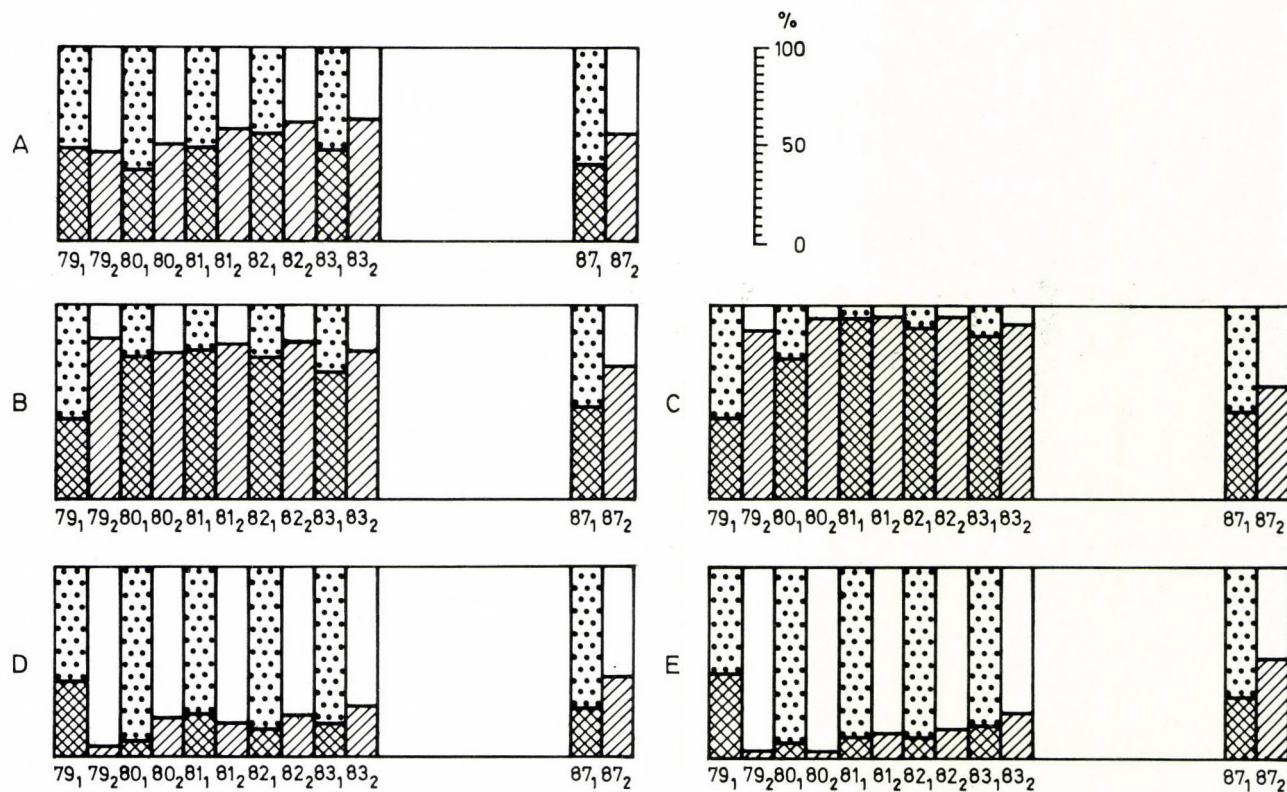
Fig. 2. Relative percentage cover of monocots and dicots. - Cross hatched lines : rel. cover % of monocots in June; Hatched lines : rel. cover % of monocots in September; Dotted lines : rel. cover % of dicots in June; Open lines : rel. cover % of dicots in September. (See Fig. 1 for explanation of symbols)

2. Species richness, diversity and evenness

2.1. Species richness

Species richness (Fig. 3) in the 5 experiments, before the treatments started, was about the same. In the control experiment little fluctuation of total number of species was detected. The species number strongly decreased after the removal of dicots and monocots and then icnreased. The tendency of changes in species number was very similar between the control experiment and the Gabonil or the Dalapon treatment with lower dose. The increase, however, was much larger in case of Dalapon 12 than in Gabonil 4.

The repeated herbicide spraying in the larger dose of Gabonil caused further considerable decrease. Similar behaviour had been observed for larger dose of Dalapon, although the effect of second spraying was much smaller. The relatively strong decrease of species number, due to the drought in 1982, showed high similarities between the control and the Gabonil 4 and Dalapon 12. The degree of decrease was 15, 17 and 11%, respectively. The extreme dry period in 1982 caused more drastic differences in species number changes in the case of larger dose of the 2 herbicides. Here the species number related to the preceding value was lower with 30%. After this drop the species richness increased again and by the summer of 1982 it nearly reached the original, initial value in every treatment excluding Gabonil 7. In 1987 there was no difference in species richness among the treatments and the drought effects brought about more or less similar deviation in each of the experiments illustrating that the differences between the treatments disappeared.

During 5 or 9 years the disturbed "communities" regained the original total number of species, but the same number did not necessarily reflect the original species composition (see Figs 2 and 3) and relative abundance of the species. It appeared that the changes in S could not be sufficiently informative considering the regeneration, the recovery of the communities as to their initial state.

2.2. Diversity and evenness

The diversity index can give a one-dimensional description of the structure of species abundance. It can be stated that there was no rough congruence between S and H (Fig. 3). The herbicides had great impact on the structure of abundance relationships, therefore the H and E could be con-
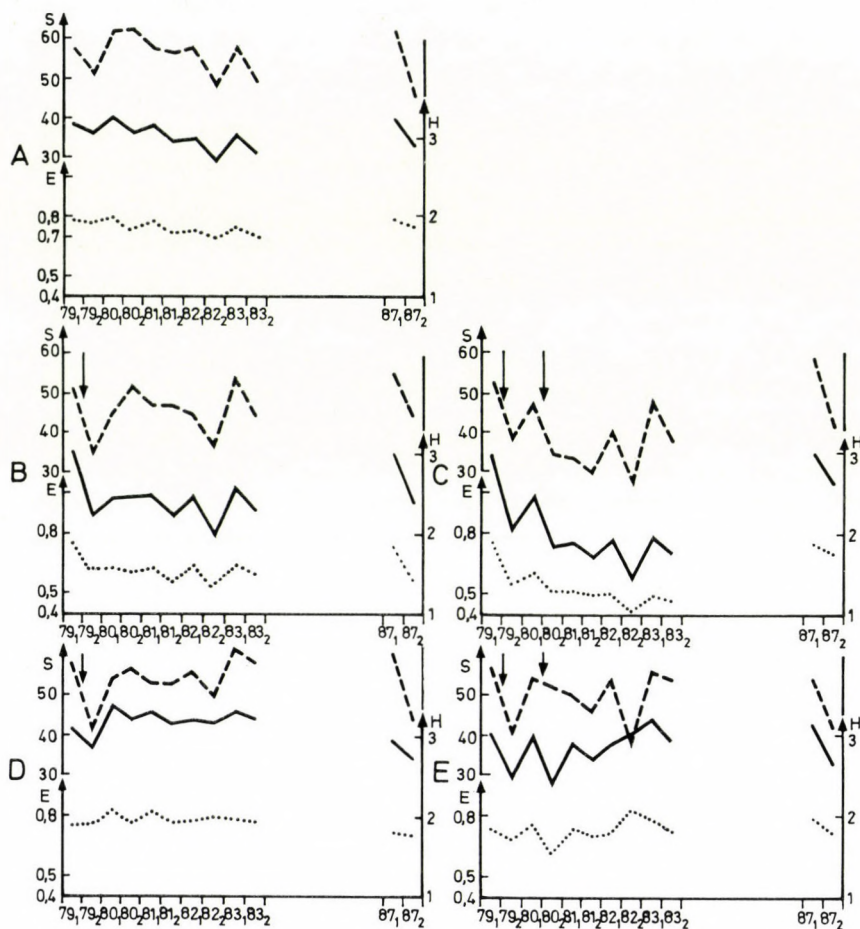
Fig. 3. Changes of species richness (S), SHANNON diversity (H) and evenness (E) (See Fig. 1 for explanation of symbols)

sidered as more important characteristics considering the response of communities to disturbance than S.

Control experiment

In the control experiment H values fluctuated within a relatively narrow range from 2.75 to 3.3. They showed a declining tendency within the first 5 years mainly due to the climatic differences between years. Seasonal fluctuations could be also well-detected. H was always higher in summer than autumn in connection with the change of E. Maximum E was reached in June

when abundance of species was relatively even and decreased in September due to the increasing dominance of some species.

Gabonil experiments

In the Gabonil experiments, removing a great number of dicots caused a strong decrease in H. After this sudden drop in case of lower dose of Gabonil the H values slightly increased and showed little fluctuation, like in the control experiment in the last 4 years studied. It indicated the effects of drought, as well as the changes in cover values of more and more re-appearing dicots influenced by yearly seasonality. During the first 5 years of the recovery period, the H values always remained much below the control level, and reached their initial values only by 1987. So, elasticity (rapidity of restoration cf. WESTMAN and O'LEARY, 1986) of this community in respect to H is lower than S.

In the Gabonil treatment with larger dose the decrease in H caused by the herbicide was much more considerable. The second spraying also caused a significant diversity decrease and a further decrease in H could be observed later over 5 years. The gradually decreasing H and increasing dominance was typical for the plots treated by Gabonil 7. The E values between 0.4-0.5 were also the lowest among the experiments indicating here the predominance of monocots and their strongly unequal abundances. After 1983 the H values tended to converge and reached their initial values in 1987, like for Gabonil 4. Nevertheless, the trends and the differences in H and E changes during the 9 years were statistically significant between Gabonil 4 and Gabonil 7 ($p = 0.01$ and 0.02) and both experiments were significantly different from the control (see Table 2).

Dalapon experiments

In case of Dalapon treatments the situation was entirely different. Although the changes of H and E values were significantly different between the two doses, but these changes were rather similar to the control (Table 2). The mean H and E values were also nearly the same as the control.

In the Dalapon 12 experiment H decreased due to the herbicide effect but later exceeded the value characteristic of the intact community. The H values were always little higher than in the control experiment. So, the degradation induced by the predominance of dicots and strong increase of some ruderal species in this experiment was indicated by H increases. H

Table 2

The results of WILCOXON's signed-ranks test for two groups, arranges as paired observations

Species richness (S), diversity (H) and evenness (E) of 2 experiments, compared over "9 years" (n=12 sampling points of time)

		Control-Gab.4	Control-Gab.7	Control-Dal.12	Control-Dal.20	Gab.4-Gab.7	Dal.12-Dal.20
S	T_s	0	0	19	3	11	0
	P	>0.10% xxx	>0.10% xxx	ns	>0.10% xxx	2% x	>0.10% xxx
H	T_s	0	0	30	17	9	5
	P	>0.10% xxx	>0.10% xxx	ns	5% x	1% x	>0.10% xxx
E	T_s	0	0	21	22	14	13
	P	>0.10% xxx	>0.10% xxx	ns	ns	2% x	1% xx

showed lower values approaching the initial value only in 1987. The drought effects were undetectable, the diversity changes indicated only seasonal fluctuation. The E values were also higher compared with the control, suggesting the relatively even abundance of many dicots. The removal of the predominant monocots and the drought effects did not cause any decrease in E. If we consider the relatively high instability and sensitivity of the coenostates dominated by dicots, it also means that in the Dalapon-treated plots the H and E values could not reflect the community "organization" and its dynamic properties such as resistance and resilience.

For the larger Dalapon dose, H and E provided stronger differences from the control than those for Dalapon 12. Drastic effects were caused by the higher dose and repeated disturbance. Owing to the herbicides, the H and the E values significantly dropped and then rapidly increased from 1981. The lower original H and E values returned again in 1987.

One of the most important differences between the Gabonil and Dalapon treatments with larger dose was that while in case of Gabonil 7 experiment the herbicide effects were followed by subsequent decreases in S and mainly in H during the first 5 years, in the Dalapon 20 experiment the increase in species number, H and E was considerable after the spraying and this quick regeneration was interrupted only for a short time by the repeated treatment.
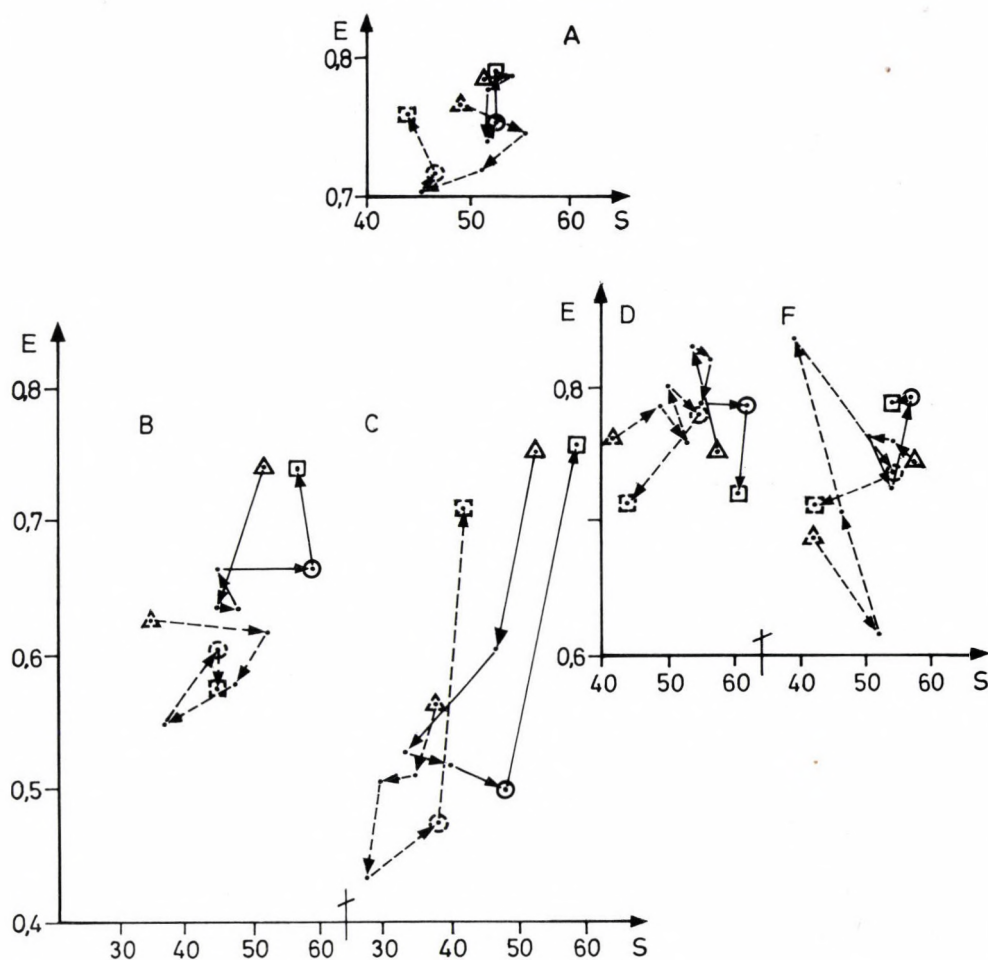
Fig. 4. Diversity phase curves. - ——: summer; -----: autumn;

△ △ 1979; ○ ○ 1983; □ □ 1987

(See Fig. 1 for explanation of symbols)

2.3. Diversity phase curves

In Fig. 4 the diversity phase curves (IZSÁK, 1982) for each treatment were presented to illustrate the simultaneous changes in E and S and the deviations from the relatively stable state, typical for control. The consecutive summer and autumn coenostates for the given sampling points of time were well-separated. Since the intact community was considered to be relatively stable, the region outlined by E and S in the control was also regarded as stable. In this quite narrow region E and S showed only little

fluctuation. Relatively high coordination and rather strong organization may be assumed.

In the treated experiments disturbance produced structural destabilization on the community level as reflected by the strong displacement of E and S from the stable state (Fig. 4). The changes of the two diversity components in Gabonil and Dalapon treatments significantly exceeded the normal amplitude of control fluctuation. The strong deviation between Gabonil experiments and the control was apparent as great decrease in S and the high heterogeneity of the changes of abundance relationships (very low E). The changes were less clear in the Dalapon experiments, but the differences from the control and Gabonil experiments were rather evident, too. It is important that the changes following herbicide spraying showed some divergence (referring to sampling plot of 5 m^2) for 5 years. At that time opposite trends between Gabonil (decrease in S, H and E) and Dalapon experiments (increase in S, H and E) were observed. The disturbed communities were able to return to their original state indicating convergence from 1983 to 1987. Although the manner and degree of the changes were entirely different at each of the treatments, the similar direction of changes, the tendency of regeneration became unambiguous (see Fig. 4, Table 6). In the phase-plane the points of H moved towards a stable region in 1987.

3. Dominance structure

Another way to express H, the relation between species richness and species dominance, is offered by dominance-diversity curves. The study of distribution of the relative abundance of species can also make it possible to give insight into the internal mechanisms of the communities. Furthermore, if the sequence of changes in the relative abundance of species, the rank order changes of species is analyzed, another aspect of community stability (see WOODS and WHITTAKER, 1981) will be described.

3.1. Dominance diversity curves

The trends of dominance-diversity cuves over 9 years according to the 5 treatments are illustrated in Fig. 5.
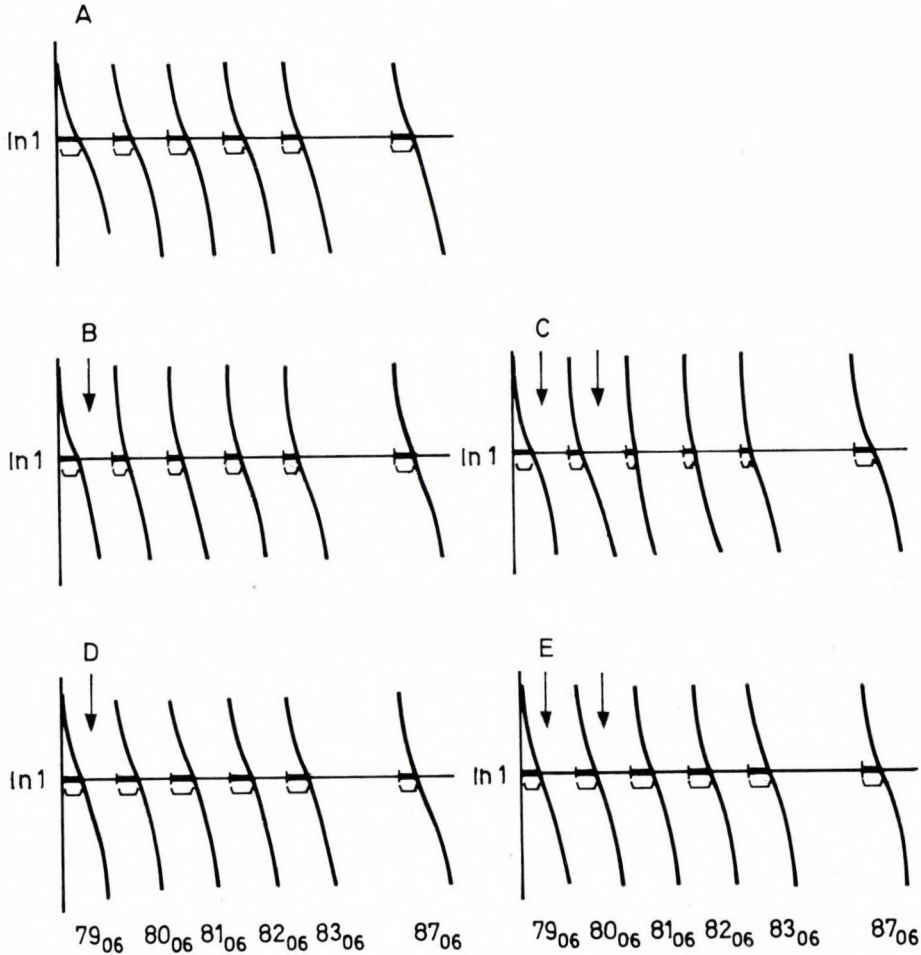
Fig. 5. Successional trends of dominance-diversity curves over 9 years. - 79_{06}: June 1979; 80_{06}: June 1980; 81_{06}: June 1981; 82_{06}: June 1982; 83_{06}: June 1983; 87_{06}: June 1987; (see Fig.1 for explanation of symbols)

Control experiment

In the control plots several species were codominant and the species number was rather high, resulting in curves nearly lognormal in shape. In this case few strong dominant species, and many species of intermediate importance value occurred. In the intact community similar patterns of species abundance were found over the 9 years. The lognormal distribution of species abundance suggests that species populations were determined by a

number of independent variables that were compounded multiplicatively (MAY, 1975; PIELOU, 1975; WHITTAKER, 1972).

Gabonil experiments

In the Gabonil experiments the dominance-diversity curve before the treatment was lognormal, like in the control. A drastic reduction in species number (Fig. 3) following the single herbicide spraying (Gabonil 4) induced a marked increase in the dominance of monocots and the unevenness of the overall distribution of abundances. Here, the surviving species after herbicide treatment partitioned quickly the bare ground (the niche-space) due to the eliminated dicots and prevented invasion by other species. As a consequence of this process one or few grasses became predominant, evenness strongly decreased, so the distribution of importance values of the species showed steep, nearly geometric dominance-diversity curves, as expected. In this situation the niche pre-emption hypotheses by WHITTAKER (1969, 1972, 1975) is acceptable. During the first 3 years of regeneration the shape of curves remained almost the same. In 1983 the dominance-diversity curve already showed a tendency towards lognormality but it became with many species of intermediate abundance similar to the initial curve only in 1987.

In case of larger Gabonil dose repeated disturbance resulted in a steeper curve. Since the reappearing of dicots was strongly restricted by the high competitive ability of the grasses for a much longer time than for the lower dose, and even in 1983 there were few species with extremely large cover, the geometric curves showed significantly steeper shapes till 1984. A lognormal curve was again approach in 1987.

Dalapon experiments

In the Dalapon experiments the overall shape of the curves demonstrates high similarity over the whole study period. The strong disturbance did not result in geometric curves. After removal of dominant species, the number of species increased and the dominance-diversity curves became again nearly lognormal in shape. There is no significant difference among the 6 curves over 9 years. A possible hypothesis concerning mechanisms behind these lognormal dominance-diversity curves is that little species interactions existed in the Dalapon-treated community and the competition of species for "space" seemed to be a more important factor in lieu of dominant monocots. As a large bare ground appeared after the disturbances a density

independent regulation is also plausible (see: "niche sharing", WHITTAKER, 1975; GILLER, 1984; DURING-WILLIEMS, 1984; BOBBINK et al., 1987).

The dominance-diversity curves were very similar in the control and Dalapon experiments, but the biological basis of these log-normal distributions was entirely different. It also appeared that the similar curves pertain to communities with strongly dissimilar species composition, structure, behaviour and stability. Dominance-diversity curves could not reflect the temporal changes of relative importance of the species involved either; that is why it was also impossible to know whether the community would be able to return to its original state or not.

3.2. Pattern of dominance sequence

The pattern of dominance sequence of the species in every treatment is demonstrated in Tables 4 and 5, where the subsequent changes with time are expressed in terms of changes in species rank order. The list of species and the abbreviations are presented in Table 3.

Table 3

List of species*

Name of species	Code of species	Name of species	Code of species
Monocotyledons		Filipendula vulgaris	Fil
		Genista tinctoria	Ge
Agrostis canina	Agr	Hieracium bauhinii	H.bau.
Anthoxanthum odoratum	Anth	Hieracium pilosella	H.pil.
Bothriochloa ischaemum	Bo	Hypericum perforatum	Hyp
Calamagrostis epigeios	Cal	Leontodon hispidus	Leon
Carex caryophyllea	Car	Myosotis stricta	Myo
Danthonia alpina	Dan.a.	Plantago lanceolata	P.lan.
Festuca rupicola	Fe	Potentilla arenaria	P.are.
Koeleria cristata	Koel	Pulsatilla nigricans	Pul
Luzula campestris	Lu	Rumex acetosella	Ru
		Saxifraga bulbifera	Sax
Dicotyledons		Seseli annuum	Se
		Teucrium chamaedrys	Teu
Achillea collina	Ach	Thymus marschallianus	Thy
Cerastium brachypetalum	Cer	Verbascum phoeniceum	Verb
Dianthus pontederae	Dian	Veronica serphyllifolia	V.ser.
Eryngium campestre	Ery	Veronica spicata	V.spi.
Euphorbia cyparissias	Euph	Viola arenaria	Vio
Euphrasia tatarica	Euphr	Viscaria vulgaris	Vis

*Only those species are listed, which occur in Tables 4 and 5.

Control experiment

In the control plots (Tables 4 and 5) the relative importance of several species remained fairly constant for the 9 year period and a relatively stable hierarchy of the species was observed. The order of the first 6-8 dominant species is the same from 1979 to 1987, and that of the other species showed only little fluctuation in dominance relations. So to the definition of stability proposed by WOODS and WHITTAKER (1981) the intact community can be considered relatively stable.

Table 4

Rank order of some species in the dominance-diversity curves

(A: Control; B: Gabonil 4; C: Gabonil 7; D: Dalapon 12; E: Dalapon 20)

	Rank number	Time of sampling					
		79_{06}	80_{06}	81_{06}	82_{06}	83_{06}	87_{06}
	1	Fe	Thy	Fe	Fe	Fe	Fe
	2	Thy	Fe	Leon	Leon	Leon	Thy
	3	Agr	Leon	Thy	Thy	Thy	Cal
	4	Car	Lu	Agr	Agr	Lu	Ach
	5	Anth	Car	Car	Car	Car	Car
A	6	Ach	Ach	Bo	Bo	Bo	Fil
	7	Bo	Agr	Lu	Lu	Ach	Bo
	8	Lu	Bo	Ach	Ach	Agr	Lu
	9	Ge	Ge	Vis	Vis	Vis	Dan.a
	10	Vis	P.are	Anth	Fil	Ge	Se
	11	Leon	Fil	Fil	H.bau	Fil	Agr
	12	P.are	Vis	P.are	Ge	Dian	H.pil

	Rank number	Time of sampling					
		79_{06}	80_{06}	81_{06}	82_{06}	83_{06}	87_{06}
	1	Fe	Fe	Fe	Fe	Fe	Fe
	2	Thy	Lu	Agr	Lu	Bo	Bo
	3	Anth	Agr	Bo	Bo	Lu	Ach
	4	Agr	Bo	Lu	Agr	Ge	Thy
	5	Ach	Ge	Anth	Car	Thy	Car
B	6	Lu	Ach	Car	Thy	Ach	Fil
	7	P.are	Thy	Thy	Ach	Agr	Ge
	8	Ge	Hyp	Ach	Ge	Dian	Dian
	9	Car	Car	Ge	Leon	Car	Lu
	10	Teu	Sax	Hyp	Dian	Leon	V.ser
	11	Bo	Euphr	Dian	Euph	Vis	Ery
	12	H.bau	Ery	Leon	Hyp	Ery	Ru

	Rank number	Time of sampling					
		79_{06}	80_{06}	81_{06}	82_{06}	83_{06}	87_{06}
	1	Fe	Fe	Fe	Fe	Fe	Fe
	2	Thy	Lu	Bo	Bo	Bo	Bo
	3	Anth	Agr	Agr	Lu	Lu	Thy
	4	Ach	Bo	Lu	Agr	Agr	Ach
	5	Car	Sax	Anth	Car	Ge	Vis
C	6	Lu	Ge	Car	Vio	Car	Car
	7	Bo	Ach	Ge	Ge	Vio	Teu
	8	Ru	Car	Vio	Koel	Ery	Lu
	9	P.are	V.ser	Dan.a	Ery	Ach	H.bau
	10	Ge	Hyp	Koel	Ach		Dian
	11	Vis	Euphr				Se
	12	Pul	Thy				Ery

Table 4 (cont.)

	Rank number	79₀₆	80₀₆	81₀₆	82₀₆	83₀₆	87₀₆
D	1	Thy	Leon	Anth	Leon	Leon	Thy
	2	Fe	Ach	Leon	H.bau	Vis	Fe
	3	Agr	P.lan	H.bau	Lu	Dian	Ach
	4	Ach	H.bau	Ach	Vis	H.bau	H.bau
	5	Anth	Vis	Lu	Ach	Lu	Vis
	6	Lu	Lu	Dian	Dian	Ach	Dian
	7	Leon	Thy	Vis	Thy	H.pil	V.spi
	8	Vis	Sax	Thy	H.pil	Se	Agr
	9	Ru	Dian	Se	Se	Fe	Se
	10	H.bau	Ge	H.pil	Ge	Thy	Pul
	11	Car	P.are	Ge	Pul	Pul	Ge
	12	P.are	Verb	Euph	Fe	Agr	Fil

	Rank number	79₀₆	80₀₆	81₀₆	82₀₆	83₀₆	87₀₆
E	1	Fe	Leon	Leon	Leon	H.bau	Fe
	2	Thy	Ach	Ach	H.bau	Leon	Thy
	3	Agr	P.lan	H.bau	H.pil	H.bau	Vis
	4	Ach	H.bau	Lu	Ach	Ach	Ach
	5	Anth	Lu	P.lan	Lu	Dian	H.bau
	6	Lu	Sax	H.pil	Dian	Lu	Dian
	7	Bo	Vis	Dian	Vis	Vis	Agr
	8	Leon	Dian	Se	Se	Se	Car
	9	P.are	Verb	Vis	Anth	Anth	Se
	10	Vis	Cer	Agr	P.lan	Fe	Pul
	11	Ge	Myo	Euph	Pul	Euph	Verb
	12	P.lan	H.pil	P.are	Euph	Pul	Ge

Table 5

Changes of rank order of some species in the dominance-diversity curves from 1979 to 1987

(A: Control; B: Gabonil 4; C: Gabonil 7; D: Dalapon 12; E: Dalapon 20)

	Species	79₀₆	80₀₆	81₀₆	82₀₆	83₀₆	87₀₆
A	Fe	1	2	1	1	1	1
	Agr	3	7	4	4	8	11
	Car	4	5	5	5	5	5
	Lu	8	4	7	7	4	8
	Bo	7	8	6	6	6	7
	Thy	2	1	3	3	3	2
	Leon	11	3	2	2	2	18
	Ach	6	6	8	8	7	4
	Ge	9	9	14	12	10	17
	Vis	10	12	9	9	9	16
	Fil	13	11	11	10	11	6
	Pul	23	20	22	20	18	-
	Se	18	16	16	13	13	10
	Dian	-	18	19	14	12	13
	H.pil	15	13	15	21	15	12

Table 5 (cont.)

	Species	Time of sampling 79_{06}	80_{06}	81_{06}	82_{06}	83_{06}	87_{06}		Species	Time of sampling 79_{06}	80_{06}	81_{06}	82_{06}	83_{06}	87_{06}
B	Fe	1	1	1	1	1	1	C	Fe	1	1	1	1	1	1
	Agr	4	3	2	4	7	18		Agr	18	3	3	4	4	14
	Car	9	9	6	5	9	5		Car	5	8	6	5	6	6
	Lu	6	2	4	2	3	9		Lu	6	2	4	3	3	8
	Bo	11	4	3	3	2	2		Bo	7	4	2	2	2	2
	Thy	2	7	7	6	5	4		Thy	2	12	-	-	-	3
	Ach	5	6	8	7	6	3		Ach	4	7	-	10	9	4
	Ge	8	5	9	8	4	7		Ge	10	6	7	7	5	13
	Vis	14	-	-	11	16	13		Vis	11	-	-	-	-	5
	Fil	19	-	-	15	13	6		Fil	-	-	-	-	-	22
	Pul	22	-	-	-	-	-		Pul	12	-	-	-	-	16
	Leon	20	-	12	9	10	-		Leon	15	-	-	-	-	-
	Se	-	14	-	-	16	14		Se	-	-	-	-	-	11
	Dian	16	13	11	10	8	8		Dian	16	-	-	-	-	10
	H.bau	12	-	-	-	-	19		H.bau	14	-	-	-	-	9
D	Fe	2	-	18	12	9	2	E	Fe	1	-	-	20	10	1
	Agr	3	-	-	25	12	8		Agr	3	-	10	-	-	7
	Lu	6	6	5	3	5	13		Lu	6	5	4	5	6	8
	Bo	14	-	-	-	-	-		Bo	7	-	-	-	-	-
	Car	11	-	23	15	16	18		Car	-	-	-	-	-	-
	Thy	1	7	8	7	10	1		Thy	2	17	19	17	13	2
	Ach	4	2	4	5	6	3		Ach	4	2	2	4	4	4
	Leon	7	1	2	1	1	-		Leon	8	1	1	1	2	-
	H.bau	10	4	3	2	4	4		H.bau	13	4	3	2	3	5
	Vis	8	5	7	4	2	5		Vis	10	7	9	7	7	3
	Dian	16	9	6	6	3	6		Dian	-	8	7	6	5	6
	Se	-	14	9	9	8	9		Se	20	15	8	8	8	9
	Pul	17	16	13	11	11	10		Pul	19	21	13	11	12	10
	Ge	13	10	11	10	15	11		Ge	11	14	16	13	18	12
	Fil	-	-	-	-	-	12		Fil	-	-	-	-	-	17

Gabonil experiments

In the Gabonil treated plots only Festuca rupicola and Festuca pseudovina have maintained their predominance, being ranked first in every year. Other monocots (Bothriochloa ischaemum, Agrostis canina, Luzula campestris) became more abundant than they were in the initial state. Most dicots disappeared and several of them became very rare (Tables 4 and 5). There are two species, Achillea collina and Genista tinctoria, that proved resistant enough to Gabonil. The rank order of these species has changed slightly during 9 years. The predominance of monocots for 4 years after disturbance is the most striking. The changes in the sequence of species are very slow,

and the rank order of the species is roughly similar to the predisturbed community only in 1987.

Dalapon experiments

In the Dalapon experiments the similar lognormal dominance-diversity curves during 9 years do not imply similar rank order of species. After spraying most of the monocots disappeared entirely. Some dicot species, such as Leontodon hispidus, Hieracium bauhinii and Plantago lanceolata, strongly spreaded vegetatively and became predominant. Several other dicots, Viscaria vulgaris, Dianthus pontederae, Pulsatilla nigricans and Seseli annuum became also more abundant than before the disturbances probably due to the absence of strongly competitive grasses. All these dicotyledonous species except for Leontodon hispidus and Plantago lanceolata maintained their higher dominance for 9 years. Thymus marschallianus became considerably less abundant than before disturbance. The strong decrease of its abundance may be attributed to the lack of shading effects of the grasses, as well as to the altered microclimate and soil moisture conditions. This species roots near the ground surface and is susceptible for withering. However, Thymus marschallianus was able to re-establish and in 1987 it was again the first or second most dominant species, like in 1979. It was also true for Festuca rupicola (Tables 4 and 5). It can be stated that the rank order of only the first 3 species (Festuca rupicola, Thymus marschallianus, Achillea collina) was the same in the community before and 9 years later after the herbicide disturbance. The relative importance of many species in 1987 was rather different from the undisturbed state indicating that although many species reappeared, their abundances were much changed.

Summary

Plant community resilience and resistance against stress situation were examined, with emphasis on different aspects of resilience and the limitation of studying community stability without comprehensive studies on recovery patterns of particular populations.

1) It was concluded that the degree of resilience (elasticity) strongly varied with the community attributes measured. Different properties of the community responded to disturbance and stress at different rates and to different degree (e.g., the different elasticity of the community in re-

Table 6

Values of some community characteristics before the treatment and 5 or 9 years later

		Control	Gabonil 4	Gabonil 7	Dalapon 12	Dalapon 20
	total cover	11801	11157	10405	11113	10631
1979	proportion of monocots	46.25 %	41.75 %	43.36 %	39.28 %	43.64 %
June	H	3.20	3.02	2.99	3.06	3.02
	E	0.7875	0.7661	0.7520	0.7516	0.7459
	total cover	13536	10902	9590	14148	12678
1983	proportion of monocots	44.17 %	63.51 %	84.81 %	17.48 %	15.65 %
June	H	3.07	2.57	1.95	3.28	3.21
	E	0.7551	0.6401	0.4994	0.7944	0.7960
	total cover	10268	9365	9251	11582	11219
1987	proportion of monocots	36.73 %	46.04 %	44.75 %	25.63 %	32.56 %
June	H	3.27	3.00	3.12	2.95	3.16
	E	0.7908	0.7416	0.7629	0.7156	0.7918

spect to species richness and total cover). One cannot meaningfully generalize the resilience behaviour of a community on the basis of one property (e.g., recovery of species richness) alone. The assessment of resilience on the basis of several community attributes may be more effective.

2) The results of this case study showed that the changes in total cover, species richness, diversity and evenness values were not sufficently informative of resilience. No strict relationship was found between H, E and resistance stability of the community; which conflicts with the findings of LEPŠ et al. (1982) in some abandoned fields. The simultaneous changes of the two diversity components (S, E), however, indicated community resistance, as well as its resilience.

The distribution of relative abundance of species was unsuitable to indicate resilience and the effects of disturbance and climatic perturbation.

Community resilience during the localized succession could be described most sufficiently by the rank order changes of some substantial species. The pattern of dominance sequence of dicots and monocots seemed to be the best sensitive indicator of restoration of the original "structure" and "function".

3) The intact community, suffering only normal temporal changes and seasonal fluctuation caused by its endogeneous dynamics in all community attributes, was found to be in dynamically stable state, which also showed resistance to drought.

The Gabonil-treated plots dominated by monocots seemed to be more resistant and less resilient than the Dalapon-treated plots. The plots dominated by dicots (Dalapon experiments) proved to be very unstable and sensitive to drought effects. The plots showed much stronger annual fluctuation in composition after disturbance (more damping cf.: FOX and FOX (1986)) than the plots with predominance of monocots.

The effects of disturbance depend upon the kind of disturbance (herbicide selective to monocots or dicots), as well as herbicide dose and frequency of treatments. The small size of disturbance and its single treatment had less impact on the vegetation than the repeated disturbance.

4) The resilience and resistance behaviour of the community without grasses or dicots was critically influenced by life history strategies, adaptive properties and other population biological features of the constituent species. Owing to the different biological properties of monocots and dicots there were great differences in the response to disturbance. Although the manner and degree of the changes were entirely different at every treatment, the similar direction of changes and the tendency of recovery was unambiguous during the investigated period. The differently disturbed community returned to its predisturbed state nearly after 9 years (Table 6) (The Pulsatillo-Festucetum rupicolae community existed in elasticity of 9 years.)

5) The trends in community changes through time and the response of the whole community to disturbance are understood in terms of processes that occurred at the population level. The response of particular populations needed inspection for an appropriate interpretation of relative ecological stability. Detailed description of population recovery patterns will be presented in a forthcoming paper.

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Acta Botanica Hungarica 35(1-4), pp. 127-143 (1989)

THE EFFECT OF SELECTIVE HERBICIDES ON TEMPORAL POPULATION PATTERNS IN AN OLD PERENNIAL GRASSLAND COMMUNITY

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(Received: 18 October 1988)

Different types of species response to herbicides and several "dynamic" categories of the species are discussed according to changes in their relative cover between 1979-1987. On the basis of different temporal population patterns and the differences in species behaviour in the intact and the treated plots, the interference relationships among the species were also identified. The study of the response of particular populations to disturbance and the recovery patterns of populations over time also contributed to understanding of community stability. Differences in the response of species to different disturbances indicated some of the important factors affecting resistance and resilience behaviour of the community and provided information on the mechanisms of regeneration.

Introduction

It is impossible to understand community resilience and resistance simply in terms of changes in floristic composition or some statistical attribute such as species diversity. The resilience of a plant community to disturbance is in fact a composite resilience of the populations, therefore additional population dynamical studies are also needed. Many recent studies have been concerned with the response of communities to various disturbances, including species removals (ALLEN and FORMAN, 1976; SUTHERLAND, 1977; ABUL-FATIH and BAZZAZ, 1979; SOUSA, 1980; HILS and VANKAT, 1982; TURNER, 1985). Species removal techniques have great advantages in studying vegetation dynamics. Experiments with species and species groups added or removed seem to be also appropriate for testing specific interactions among community components under natural conditions (FOWLER, 1981; FOWLER and ANTONOVICS, 1981; SILANDER and ANTONOVICS, 1982; FONTEYN and MAHALL, 1981; MITCHLEY and GRUBB, 1986). Ultimately, of course, the pattern of interference or competition among species can be one of the factors which determine community structure and regulate regeneration processes after disturbance or perturbation.

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In this paper I continue the study of herbicide-disturbances on vegetation dynamics and relative ecological stability relations in a perennial grassland community. At the community level, pattern of vegetation change induced by herbicide treatments was evaluated with multivariate analyses (VIRÁGH, 1986) and the temporal change of total cover, species richness, diversity and evenness was also measured (VIRÁGH, 1988). The effects of the selective removal of dicots and monocots on population patterns are presented here. Population recovery patterns in 5 different experiments will be discussed in detail. Problems examined include:

- What are the temporal abundance patterns of populations?
- Do population patterns reflect species strategies?
- What interactions among populations are suggested by the patterns?

The species removal approach for describing the mechanism of regeneration is also taken.

Materials and Methods

Field study

Experimental disturbances were carried out in a secondary steppe community in NE-Hungary. A homogeneous stand of a Pulsatillo-Festucetum rupicolae community near the stable state was selected for studies of local secondary succession, i.e., regenerational processes initiated by some leaf-herbicide treatments.

Dominant and subordinate species were removed within five 2.25 m^2 permanent plots by selective herbicides. Grasses and sedges were killed with Dalapon (2,2-dichloropropionic acid) and dicots with Gabonil (2,4-dichlorophenoxyacetic acid). Treatments were used in two doses. A detailed description of experiments and sampling design is given in VIRÁGH (1982, 1987).

Data

In order to follow the response of populations during the 9 years, percentage cover of each species, visually estimated, was summed over for all the quadrats of each individual treatment. Consequently, variation between the 5 replicate plots did not influence the results, only the temporal changes of cover in each treatment and the cover differences between the control and treated quadrats were evaluated.

Methods

The present investigations rely on cover changes. It was expected that plant cover by its high plasticity would be better indicator of the effects of disturbance than the number of individuals.

Relative cover values of some species were plotted against time to examine pattern of change during a 9 year period. Several dynamic categories of species were set up.

Following the removal of particular species groups (monocots, dicots) from the community, the remaining species may respond through faster or slower vegetative growth, or an

increase or decrease of abundance or both (see also FOWLER, 1981). So from these responses and from the differences being in the species behaviour in the intact and treated plots without grasses or dicots, the cases of interference, in the broad sense, were also identified.

Results and Discussion

In describing the processes which occur at the population level and control the trends in community changes, I distinguish processes, which appear to maintain a dynamically stable state of the original community, from those which seem to facilitate recovery of the community after disturbances: "maintenance dynamics" as opposed to regeneration dynamics.

In the closed, very dense intact grassland community a large number of species coexisted (species richness is about 100). Very few species made up most of the plant cover and many rare and poorly represented species could be found. The community was dominated by perennial long-lived species. The annual species accounted for 10%, but these had only a 2-3% share in the total cover. It was concluded (VIRÁGH, 1988) that the annual variation in species composition and in the relative "importance" of the species was relatively little. The position of several species was constant over 9 years and a relatively fixed species hierarchy was observed in the community. Some trend in relative cover changes of species between 1979 and 1987 could also be detected in the intact community. The trends in population dynamics of some species through time are presented in Fig. 1.

Six dynamic species categories were recorded:

1) decreasing (Agrostis canina, Potentialla arenaria, Rumex acetosella)
2) increasing (Dianthus pontederae, Filipendula vulgaris, Hieracium bauhinii, Seseli annuum)
3-4) persistent - stable (Viscaria vulgaris, Euphorbia cyparissias)
   - oscillating (Carex caryophyllea, Luzula campestris) or indicating seasonal fluctuation (Bothriochloa ischaemum, Thymus marschallianus)
5) parabolic form (Achillea collina, Leontodon hispidus, Festuca rupicola)
6) bimodality (Genista tinctoria).

Different life strategies, competitive ability, reproductive capability, different tolerance to climatic changes, for example, can be reflected in these population patterns. The most significant influential factor in the grassland community may be the variation of climatic conditions between years and within a year. Ultimately, in spite of the annual changes and the
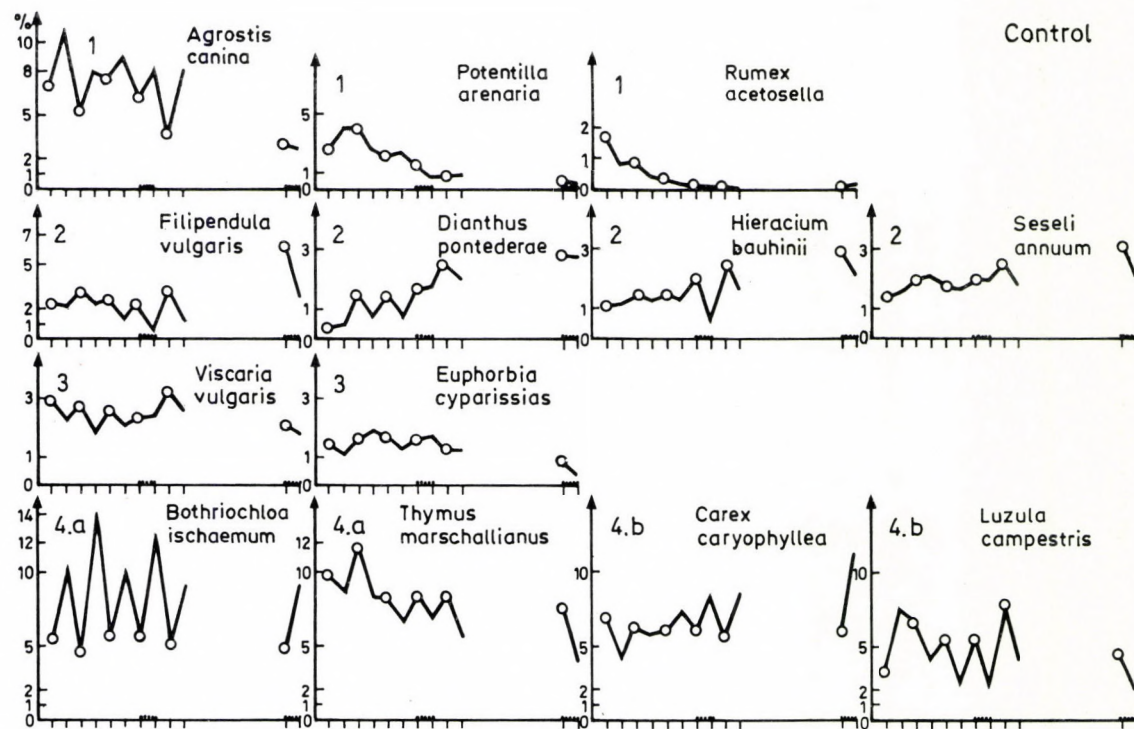
Fig. 1. Trends in relative cover changes of some species in the control experiment during 9 years. - 1: decreasing; 2: increasing; 3: stable; 4a: fluctuating; 4b: oscillating; 5: parabolic form; 6: bimodality. - 79_1: June 1979; 79_2: Sept. 1979; 80_1: June 1980; 80_2: Sept. 1980; 81_1: June 1981; 81_2: Sept. 1981; 82_1: June 1982; 82_2: Sept. 1982; 83_1: June 1983; 83_2: Sept. 1983; 87_1: June 1987; 87_2: Sept. 1987. - Dotted lines indicate drought periods

5
Achillea collina
5
Leontodon hispidus
5
Festuca rupicola
6
Genista tinctoria
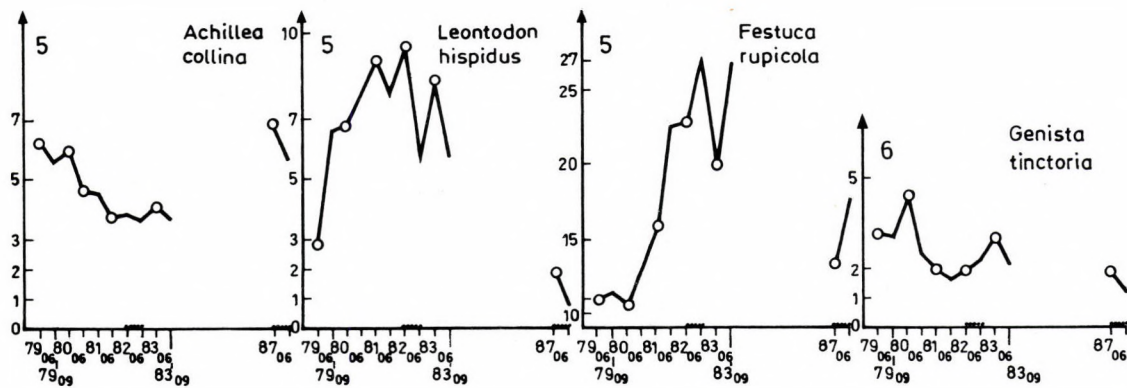
Fig. 1 (cont.)

various individualistic feature of the component species the community was able to maintain a relatively constant species composition with very similar abundance-dominance relations for a long time, as already discussed earlier.

The treated plots were reinvaded by species of the original community and the disturbed quadrats returned to their previous state about 9 years after disturbance. Recovery was mainly determined by adaptive strategies of surviving species. Following the removal of species large bare ground appeared, where the expansion of vegetatively well-spreading species was the most typical phenomenon. Very few species regenerated from seeds in the soil and few species invaded from the neighbouring plots (VIRÁGH and GERENCSÉR, 1988). Some species disappeared probably due to the increase of bare ground and the changes in light conditions, temperature and soil moisture. This early stage of regeneration was mainly determined by "competition for space" (YODZIS, 1978). The later changes limited the area of bare ground, newly available resources and nutrient supply. More and more species reappeared from the third growing season following disturbance and different stages succeeded each other through relatively short time-intervals. The dominance and abundance relationships among the species also considerably changed and more than 5 years later they tended to approximate their predisturbed state. In this phase interference and some weak interspecific interaction among the species can also be supposed to control the changes.

Two types of selective herbicides caused different changes by removing the monocots or the dicots. Owing to the different biological properties of these groups there were great differences in responses to disturbance and recovery pattern of the remaining and the re-appearing populations. In general 8 patterns of response to herbicide treatments can be distinguished (Fig. 2).

In the first 4 patterns disturbance causes significant cover decrease, and the other patterns reflect the opposite behaviour.

Species cover continuously increased but never reached the original (control) level (Pattern A), increased to original level (Pattern B), increased above original level (Pattern C) and remained much below the original level for a relatively long time and then increased slowly (Pattern D). Cover exceeded the original values and then declined to the original level (Pattern E), strongly exceeded the original level and then suddenly decreased approaching the original level (Pattern F), increased and hardly
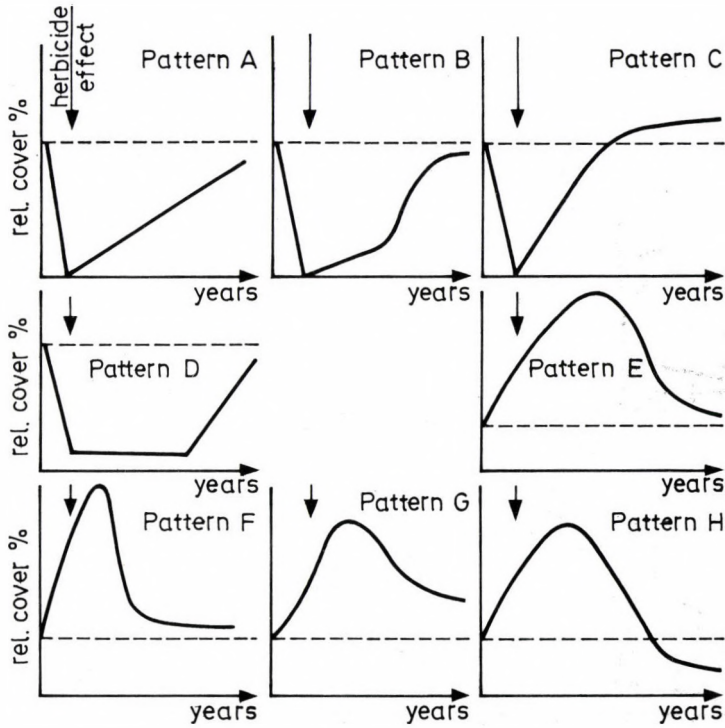
Fig. 2. Recovery patterns of species-populations in disturbed plots (Dashed line indicates total cover of species in the original intact state before herbicide spraying.) (See the text for explanation of Pattern A - Pattern H)

Gabonil

rel. %
herbicide effect
herbicide effect

A

a Hieracium bauhinii

a Pulsatilla nigricans

a Potentilla arenaria

a Teucrium chamaedrys

b Thymus marschallianus

b Dianthus pontederae

b Filipendula vulgaris

b Euphorbia cyparissias

b Leontodon hispidus

b Carlina vulgaris

b Plantago lanceolata
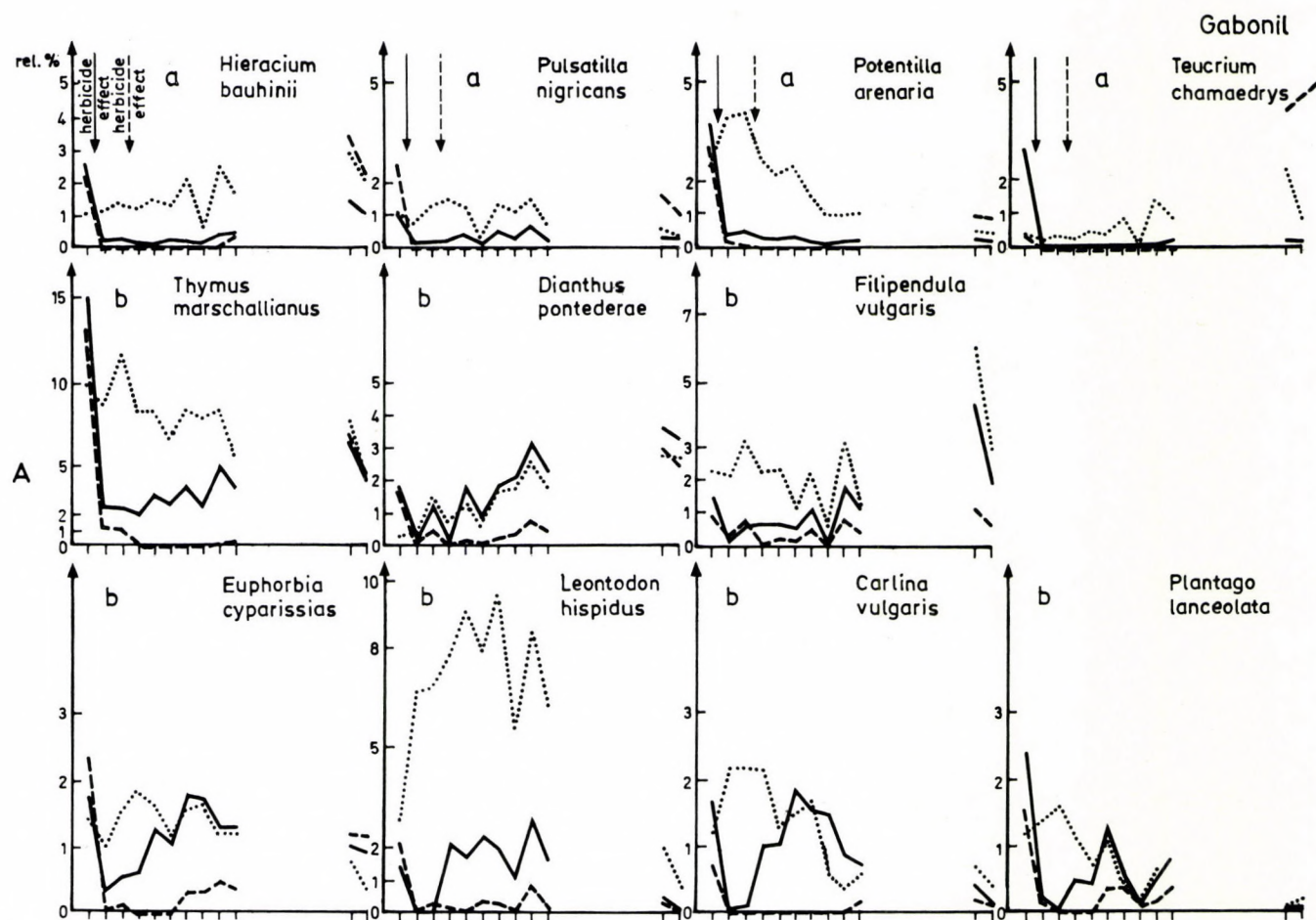
Fig. 3a. Different types of species response to Gabonil herbicide and species reactions after disturbance over a period of 9 years. Response of dicots; a: very sensitive group of species, b: sensitive species, c: moderate sensitivity of group of species, d: species group, more or less tolerant to Gabonil
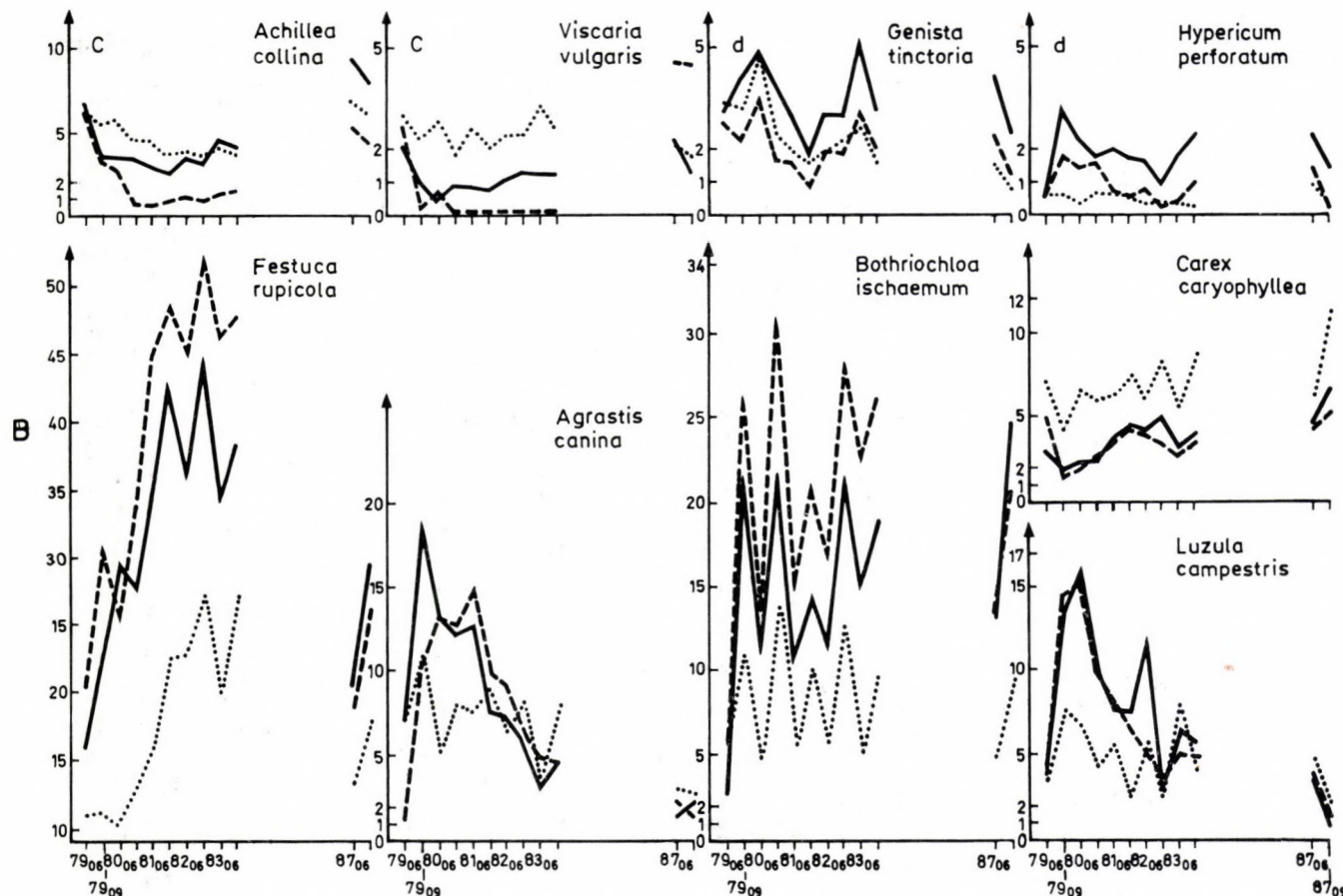
Fig. 3b. Different types of species response to Gabonil herbicide and species reactions after disturbance over a period of 9 years. Different types of monocot reaction throught time

(—— Gabonil 4; ----- Gabonil 7; ..... Control) (See Fig. 1 for explanation of symbols)
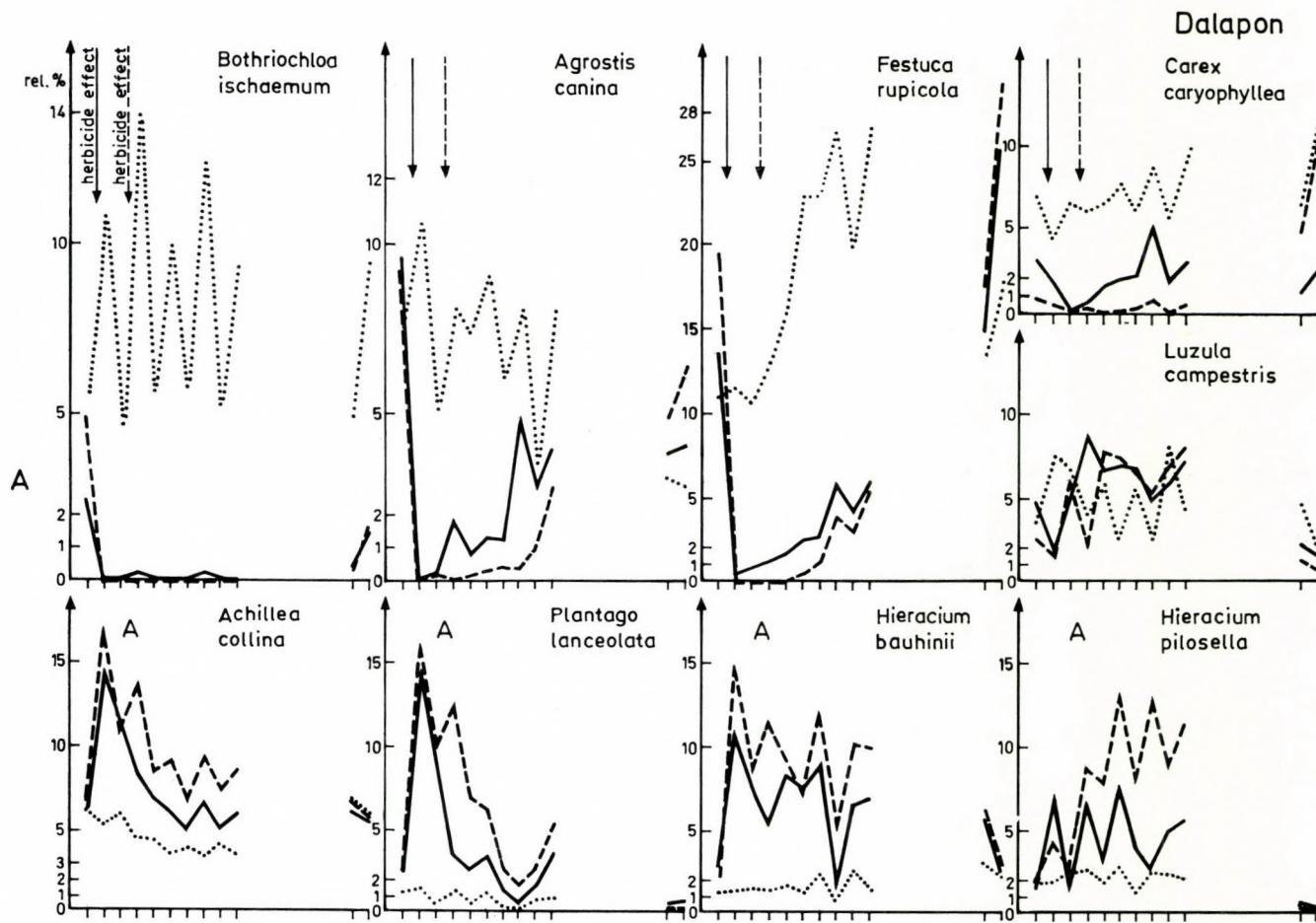
Fig. 4a. Some typical forms of species reactions after Dalapon treatments. Response of the most important monocots to Dalapon herbicide
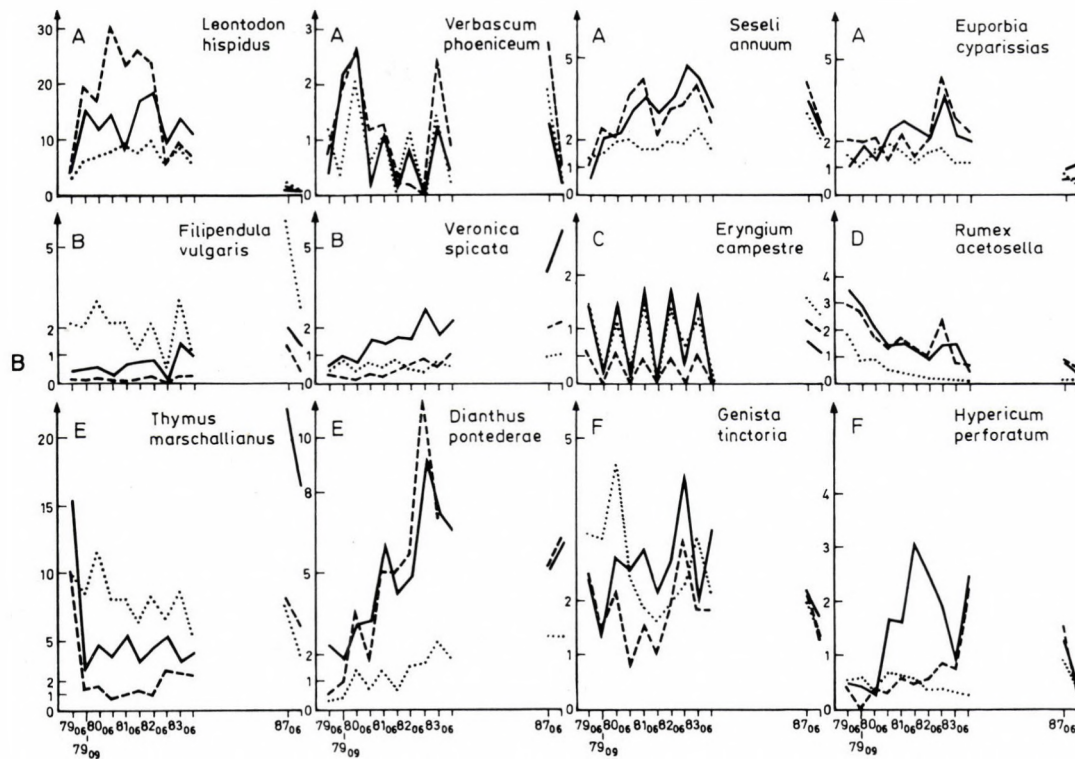
Fig. 4b. Some typical forms of species reactions after Dalapon treatment. Recovery pattern of dicot species in Dalapon-treated plots during 9 years; (Six groups (Type A - Type F) were distinguished: see the text). (See Fig. 1 for explanation of symbols.) (——— Dalapon 12; ----- Dalapon 20; ..... Control)

decreased later (Pattern G) and strongly increased and then collapsed or decreased significantly below the original level.

Now some typical forms of species response to herbicides and trends in species population dynamics after disturbances over 9 years are presented. Relative cover of species is illustrated (Figs 3 and 4) to express also the relationships among the species. In Figs 3 and 4 the different population patterns in the case of 2 herbicide doses and their similarity to control patterns are also presented.

Gabonil treatments

The dicotyledonous species were unequally sensitive to Gabonil. Four large groups of species regarding their sensitivitiy to the herbicide and their later changes through time were distinguished (Fig. 3).

Pattern "a" was represented by the very sensitive group of species (Hieracium bauhinii, Pulsatilla nigricans, Potentilla arenaria, Teucrium chamaedrys). Pattern "b" was shown by some sensitive species, mostly ruderals (Leontodon hispidus, Plantago lanceolata, Euphorbia cyparissias, Carline vulgaris, etc.). These species explosively increased in their cover after the initial drastic decreases due to the direct effect of herbicide. Their behaviour can be explained by their morphology (the possession of rhyzomes, long stolons or rooting stems). The species belonging to the third group (Pattern "c") (Achillea collina, Viscaria vulgaris) showed moderate sensitivity to Gabonil. The species of the last group (Pattern "d") appeared more or less tolerant to the herbicide. Marked relative cover increase of Genista tinctoria and Hypericum perforatum immediately after herbicide spraying was followed by significant decrease and then they again reached a high peak. Both species strongly increased above the control level and slowly decreased later.

It is obvious that the removal of all the dicots produced significant increases in the monocot populations. Different types of monocot reaction through time demonstrated in Fig. 3 show the effects of competition among the monocotyledonous species. Continuous increase of one or more monocots could be limited by expansion of other species, for which the population dynamics of Agrostis canina and Luzula campestris, as well as antagonism between Carex caryophyllea and Luzula campestris serve as good examples.

In these experiments a relatively slow regeneration appeared. Nine or five years were required at least for "complete" recovery of most species

(cf.: Fig. 3). Reappearance of the dicot species belonging to the very sensitive group (Pattern "a") was quite impossible during the first 5 years of secondary succession. Germination of many dicots seemed to be suppressed during the early phase of regeneration, though the buried seed bank in the soil with numerous dicot seeds provided possibility for the dicots to reestablish (VIRÁGH and GERENCSÉR, 1988). Germination of seeds of some species was probably inhibited by the expansion of strong competitive monocots and the altered microclimate and leaf cover conditions over the treated plots. Vegetative way of regeneration was supposed for many dicots (Eryngium campestre, Achillea collina, Leontodon hispidus, Genista tinctoria, Carlina vulgaris, Euphorbia cyparissias) invading into the quadrats or increasing their cover mostly vegetatively. This hypothesis was supported by these species showing cover increase after herbicide disturbance but whose seeds were completely absent from the soil seed bank even 2 years after the treatment.

Dalapon treatments

After removal of all monocots, different groups of dicotyledonous species adapted to regenerate. In these experiments the rapid vegetative spreading of some dicots was the most characteristic. Regenerative vigour from seeds of these species was very little. There was a marked hierarchy among the "Dalapon-followers", with Leontodon hispidus, Plantago lanceolata, Hieracium bauhinii, Hieracium pilosella, Achillea collina being particularly prominent first as they are in many strongly degraded communities.

According to their recovery pattern between 1979 and 1987, the dicot species were divided into 6 groups (Fig. 4) as follows:

Type A: Very strong relative cover increase induced by absence of the strong competitor grasses, then significant decrease (Plantago lanceolata, Potentilla arenaria, Achillea collina, Leontodon hispidus, Hieracium bauhinii and H. pilosella, Seseli varium, Euphorbia cyparissias, Verbascum phoeniceum).

The species belonging to this group became dominant because of their superior colonizing ability and were suppressed by other component species one or few years later after disturbance. The decline of these species could be attributed to their low competitive capability or poor ability to tolerate interference. They were also limited in the dense natural community.

Type B: Relative cover increase immediately after disturbance with gradual increase further on (Filipendula vulgaris, Veronica spicata).

Type C: Fluctuating species (Eryngium campestre).

Type D: Gradual decrease during regeneration (Rumex acetosella).

Type E: Decrease in relative cover then gradual increase (Dianthus pontederae, Thymus marschallianus).

Type F: Decrease in relative cover, then gradual increase and later again decrease (Genista tinctoria, Hypericum perforatum).

The response of the five most important monocots to Dalapon is demonstrated in Fig. 4. Reappearance of grasses was possible only from the third year of the secondary succession. Regeneration of monocots mainly from seeds was very slow because of the absence of persistent seed bank in the soil and fresh graminoid seed input following disturbance.

Conclusions

This study attempted to illustrate temporal population patterns in a perennial grassland after different disturbances. The trends presented here may be summarized by referring to the three major questions posed initially:

1) Each population showed special patterns of cover change within the intact community. Annual fluctuations could be caused by specific individualistic features of species and different population dynamical processes intrinsic to the community.

The species strongly differed in their response to disturbance and recovery patterns. "Population curves" also indicated marked differences for the two herbicide doses. There were only few species, such as Verbascum phoeniceum, Dianthus pontederae, Filipendula vulgaris and Genista tinctoria, whose cover changes seemed to be independent of herbicide level. Many species that indicate drought were also detected on the basis of their cover changes, which were similar in each experiment. These species were Luzula campestris, Plantago lanceolata, Filipendula vulgaris and Leontodon hispidus (Figs 1, 3 and 4).

2) The patterns reflected different life or propagation strategies and suggested different adaptations to regeneration (Figs 3 and 4). The most effective colonizers were those with rapidly spreading vegetative propagula and high ability to occupy the bare ground.

3) Different temporal patterns and the differences in species behaviour in the intact and the treated plots reflected the interactions and the interference relationships among the populations. The growth of many dicots (see Fig. 4) was limited in the original dense community, but these species were able to increase significantly in the absence of the strong competitor grasses. The increase of dicots was primarily due to the fact that they require bare ground for their growing. The monocots also expanded when interspecific competition between monocots and dicots was weakened by removal of many dicots (Fig. 3). On the contrary, some species (Thymus marschallianus, Dianthus pontederae) preferred the dense, well-developed structure of the intact grassland community, and they decreased sharply when this structure was reduced by both types of herbicides.

It must be noted that the intensity of competition among the species was based on relative cover changes following the removal of a certain group of species. Hence, a high level of uncertainty associated, of course, with the estimated responses to multispecies removals. Some very reasons of this uncertainty may be species group removals instead of a single species removal and the occurrence of high-order relationships among the large number of the species in the community.

This study also aimed to detect the result of recovery (resilience of the community) at population level. It appeared that according to the original level (before the spraying), most of the recovery patterns belong to the general pattern B, E and F (see Fig. 2 and cf. Figs 3 and 4). Despite of significant changes in relative cover after treatments and the great differences in responses to disturbance most species returned to their predisturbed state (in respect to their cover values) during 9 years. It was concluded that recovery patterns of populations well-indicated the result of regeneration.

The results obtained by comparing the population patterns in the treated and non-treated plots were also useful to formulate some hypothesis about the mechanisms of regeneration. Dalapon effects involving removal of the most abundant and dominant monocots suggested that the grasses occupied as much area as they could. Removal of the monocots led to strongly significant increases in the cover of many dicots will a cover of 0.5% or more (2-3%) in the control state, but removal of the less abundant dicots led to much smaller change in the cover of monocots (see Figs 3 and 4).

In general, disturbances produced bare ground in which regeneration, i.e. a local secondary succession was initiated. Since the community con-

tained a relatively small persistent seed bank, its recovery was mainly determined by vegetative regeneration. The pattern of regeneration and colonization observed in the experiments strongly supported GLEASON's (1927) individualistic concept (cf.: GLENN-LEVIN, 1980; PICKETT, 1982; BELSKY, 1986) and implied the validity of population-centered explanation of community phenomena. The individualistic-specific temporal pattern of populations suggested different adaptation and response as "some causal mechanism" also for community pattern.

In lieu of a comprehensive study population interactions and species strategies, this "population study" remains at the descriptive level and much of the information presented here refers necessarily to "patterns". For a better interpretation of the changes at population level, the interaction of all stages of the life cycle with changes in weather and variation in soil surface characteristics, as well as resource level, which might explain some of the population patterns, have to be studied. Moreover, some additional ecophysiological and demographic analysis are also needed.

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Acta Botanica Hungarica 35(1-4), pp. 145-160 (1989)

SHORT TERM STRUCTURAL CHANGES IN SANDY GRASSLAND COMMUNITIES

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(Received: 15 June, 1988)

Structural changes in three communities of a mosaic-like sandy grassland were studied in a 6 year period. The investigations were carried out in permanent quadrats on 13 representative sites. In the first approach we evaluated the many year data of only one season in order to establish the annual dynamics of alterations.

The stands representing the three communities formed distinct group in every year in the multivariate analyses. In the late samples, however, the character of communities approached each other.

The most effective factor on the succession of psammophile grasslands is the available water quantity. The very fluctuating distribution of precipitation in the examined period had a strong correlation with the structural changes of the vegetation. The dry period induced a strong stress mainly for the mesothermic community of grooves, therefore very pronounced alterations were observed in these sites.

Keywords: Bugac, climate, sandy grassland, succession, vegetation dynamics

Introduction

The directing and regulating functions that assure the stable existence of plant populations are known fairly well and have been studied extensively. It is enough to refer to the comprehensive work of HARPER (1977) or GREIG-SMITH (1983) instead of the long enumeration of the corresponding papers.

The questions of the organization of plant communities, the laws of the development of their structure have been in the centre of researches for a long period, only the Hungarian extensive literature is summarized in the bibliography by SOÓ (1978).

Among the papers on the structural changes of stands, the structural rearrangements due to the effect of the changing environmental conditions, it is worth mentioning the researches that have been started in our country in the second half of 70s. PRÉCSÉNYI (1980) described the successional series on the basis of diversity changes in case of the progressive series of a sandy grassland. FEKETE and VIRÁGH give a picture of the changes in

composition and diversity during the secondary succession of a mountaineous xeroseries (FEKETE and VIRÁGH, 1982; VIRÁGH and FEKETE, 1984).

The course of the quick change of species composition on a flood-plain biotop, mainly with a multivariate approach, is demonstrated by BAGI and BODROGKÖZY (1984) as well as by BAGI and KÖRMÖCZI (1986).

The phenetic changes and the transformations of niche structures can be used as another way for following the successional steps (FEKETE and MELKÓ, 1981; MELKÓ, 1983; PRÉCSÉNYI et al., 1977; PRÉCSÉNYI et al., 1979; PRÉCSÉNYI et al., 1980).

In this paper, joining with the studies mentioned above, we try to establish the connection between the change of vegetation structure and the presumably background factors of the environment. Since among the environmental factors, the seasonal dynamics of the phytomass in the sandy grassland is mainly influenced by certain climatic parameters (KOVÁCS-LÁNG, 1974), furthermore the individual successional processes are determined by the water state of the soil (HOKKANEN and RAATIKAINEN, 1977), in the present case I have also deemed it advisable to search for the traces of the short-term climatic changes in the successional states of vegetation.

Materials and Methods

The investigations of the stand structure were carried out on the sampling plot of the Zoological Department of József Attila University in Bugac, Kiskunság National Park. The phytosociological relevés were taken in the immediate vicinity of the zoological sampling points in order to make a comparision. The map of the sampling area is shown in Fig. 1. The individual sampling sites are demonstrated in it, their numbers are in accordance with those used by zoologists (GALLÉ et al., 1985).

The investigations were performed on 14 sampling points representing four plant communities. These are as follows: Festucetum vaginatae danubiale (KÁRPÁTI I. 54) (henceforth abbreviated as FV), Potentillo-Festucetum pseudovinae Bodrk. 59 (PFP), Molinio-Salicetum rosmarinifoliae (SOÓ 33) 57 (MSR), Brometum tectorum secaletosum (SOÓ 25) Bojkó 34. As the latter one was represented only by one single sampling point (No. 8), it was neglected during the evaluation of the results.

The phytosociological relevés were surveyed in quadrats of 4 m^2 on the sampling sites in three years (1981, 1985 and 1986). The relevés were taken during the late spring period, at the end of May or the beginning of June.

The relative cover values of vegetation are shown in Table 2. (The species being insignificant from the point of view of the subsequent analyses are not displaced in it.)

Multivariate analyses were used to evaluate the basic data on COMMODORE-64 microcomputer with BASIC-Programs.

CZEKANOWSKI's similarity index and the Euclidean distance were applied in the cluster analysis. The fusion was made by the group-average algorithm (PODANI, 1980). Principal component analysis was used for the ordination of objects which was based on the correlation matrix of basic data (PIELOU, 1984).

The diversity of the individual stands was calculated by means of the Shannon diversity index.

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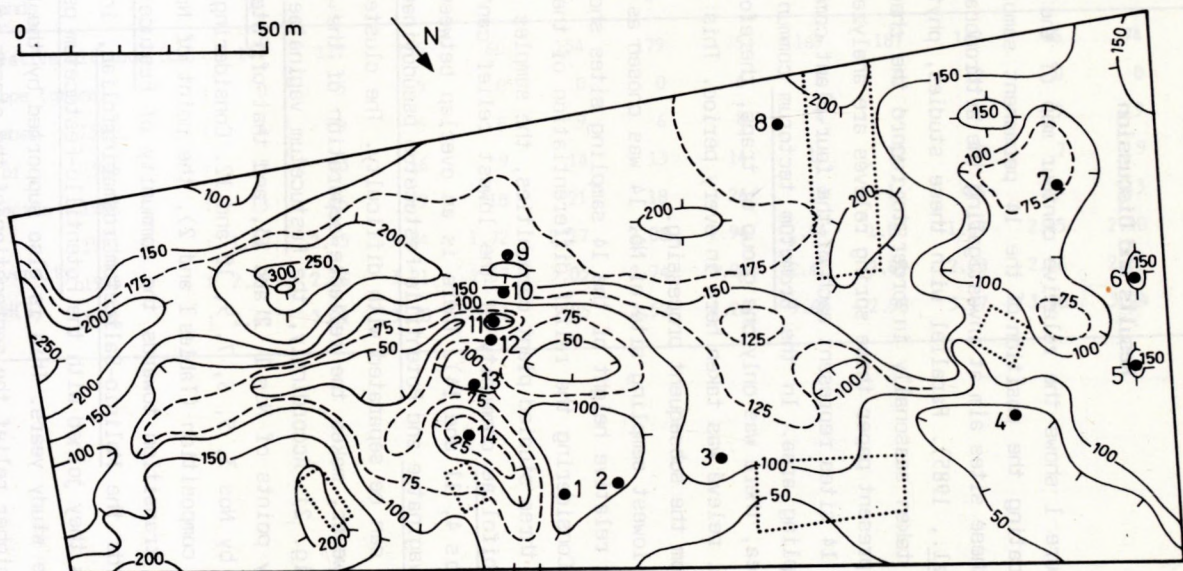
Fig. 1

The climate diagram (Fig. 6) made for the evaluation of the results was constructed on the basis of data measured at the meteorological station in Kecskemét. The monthly average of temperature and the monthly amounts of rainfall between 1977 and 1988 are demonstrated in the figure.

Results and Discussion

Figure 1 shows the relative contour map of the Bugac examination area, indicating the position of the 14 permanent sampling sites. Traps placed on these sites aim at investigating the arthropoda fauna of the area (GALLÉ et al., 1985). Parallel with these studies, phytosociological relevés were taken seasonally in order to record the changes of the vegetation. In present paper three spring relevés are analyzed.

The 14 sites represent each of the four plant communities occurring on the sampling area. In the Brometum tectorum community occupying the smallest area, there was only one group of traps, therefore only one phytosociological relevé was taken here in every period. This sample, No. 8, was excluded from the subsequent processing.

The lowest sampling site of No. 14 was chosen as a reference point so that the relative height of the 14 sampling sites should be determined (Table 1). Considering the relief differentiation of the points which represent the three studied plant communities, the samples in Molinio-Salicetum rosmarinifoliae community of the lowest relief can unambiguously be isolated (Nos 4, 11 and 14). There is an overlap between the samples of Festucetum vaginatae and Potentillo-Festucetum pseudovinae along the relief height they can be separated with difficulty. The cluster analysis of the samples, however, makes the reliable separation of the individual stands possible (Fig. 2). Accordingly, the Festucetum vaginatae community is represented by points of Nos 1, 2 and 13, and that of Potentillo-Festucetum pseudovinae by Nos 3, 5, 6, 7, 9, 10 and 12. Considering the exposure and the species composition (Tables 1 and 2), the point of No. 3 is likely to represent a transition towards the community of Festucetum vaginatae and No. 7 towards the Molinio-Salicetum rosmarinifoliae, in the dendrograms nevertheless they joined with the Potentillo-Festucetum pseudovinae in each of the three study years. This is also supported by the PCA results (Fig. 3). On the higher relief the segregation of the stands is affected not only by the relative height, but by the other relief conditions, too. While the stands of the Potentillo-Festucetum pseudovinae cover larger flat areas, in

Table 1

Relative altitude and slope of sampling sites and the changes of species number and diversity in the experimental years

Stands			1	2	3	4	5	6	7	8	9	10	11	12	13	14
relative altitude (cm)		:	147	127	135	60	154	179	75	169	187	147	45	74	131	0
slope (grade)		:	0	5	5	0	0	0	6	5	0	12	0	0	4	0
number	1981	:	6	9	5	8	9	6	8	4	7	6	7	9	6	8
of	1985	:	12	13	16	9	14	13	14	11	12	10	7	9	14	11
species	1986	:	13	15	19	18	21	18	26	18	16	16	17	13	15	17
diversity H(S)	1981	:	1.80	2.45	1.84	1.72	2.17	2.00	1.94	1.44	1.80	1.67	2.45	2.10	1.33	2.43
	1985	:	2.22	2.76	3.21	2.57	3.05	2.74	3.06	2.42	2.89	2.20	2.36	2.65	3.18	2.96
	1986	:	2.67	3.21	3.70	3.61	3.85	3.52	4.26	3.68	2.98	3.17	3.28	3.24	3.09	3.35

84,03
1981
0
1 13 2 3 5 10 7 9 12 6 4 11 14 8
52,14
1985
0
1 13 8 2 9 3 5 12 6 10 7 4 11 14
41,02
1986
0
1 13 2 12 3 7 8 5 6 10 4 14 11 9
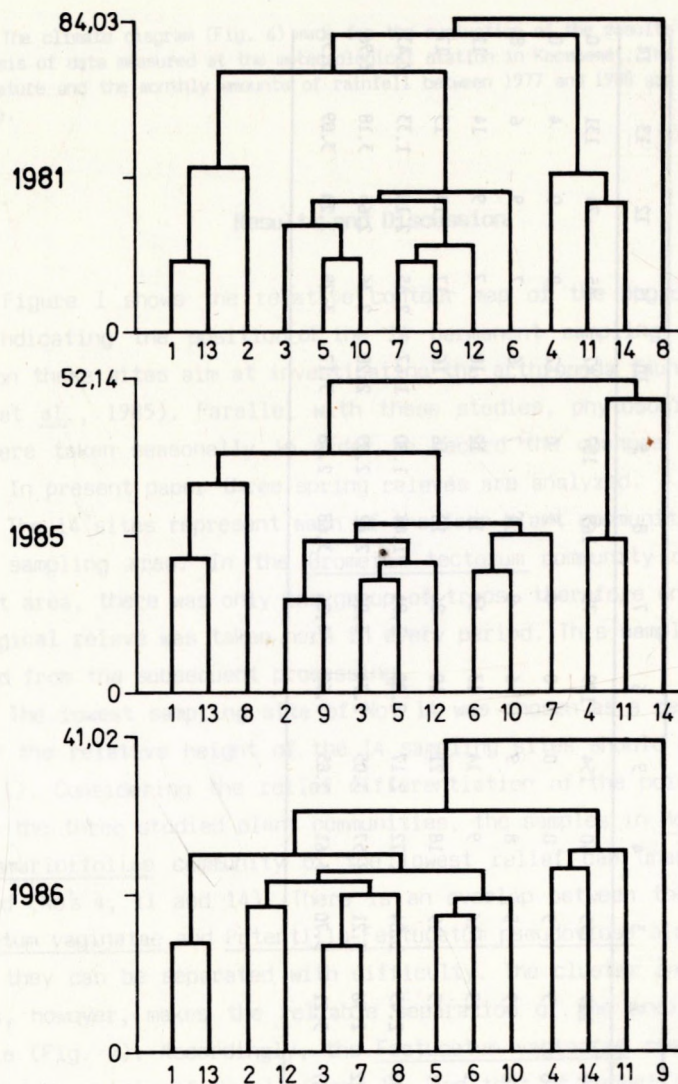
Fig. 2
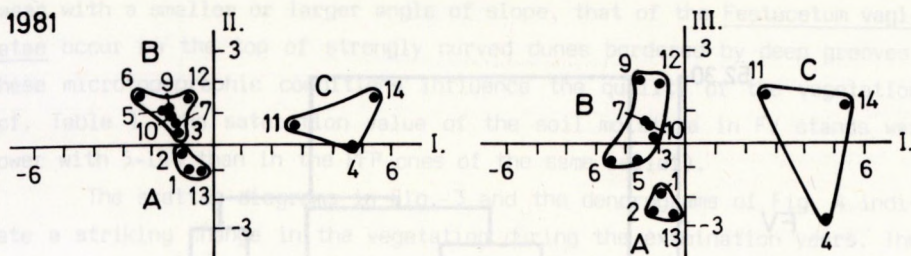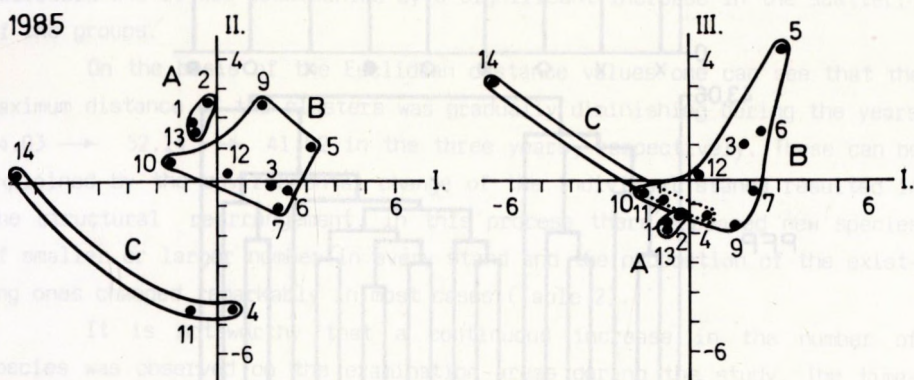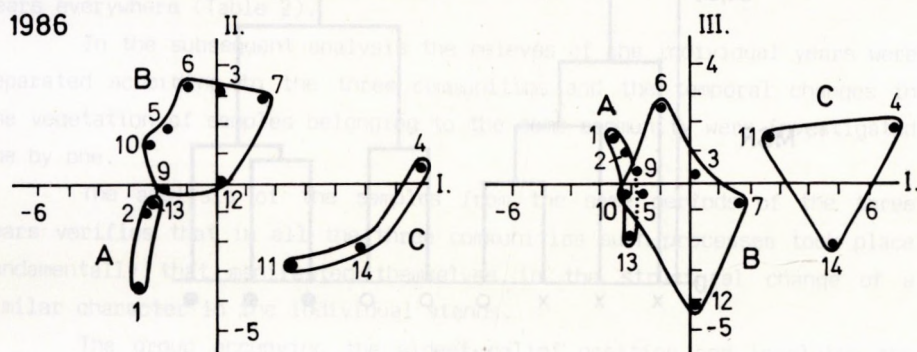
Fig. 3
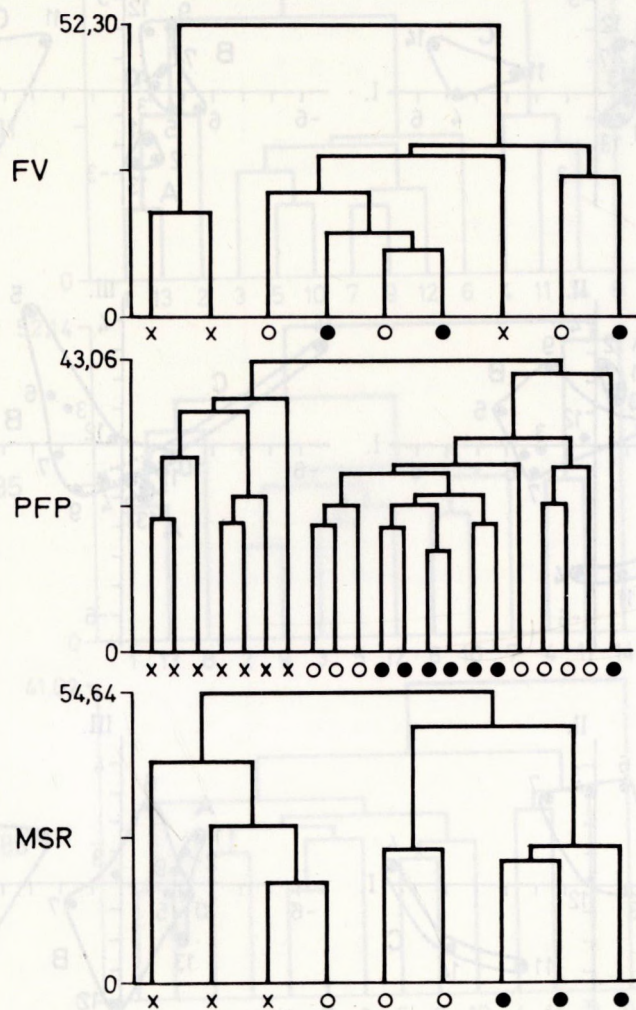
Fig. 4

cases with a smaller or larger angle of slope, that of the Festucetum vaginatae occur on the top of strongly curved dunes bordered by deep grooves. These microtopographic conditions influence the quality of the vegetation (cf. Table 1, the saturation value of the soil moisture in FV stands was lower with 5-10% than in the PFP ones of the same relief).

The scatter diagrams in Fig. 3 and the dendrograms of Fig. 4 indicate a striking change in the vegetation during the examination years. The distance of the weight points of the sample groups in the PCA factor space decreased and it was accompanied by a significant increase in the scattering of the groups.

On the basis of the Euclidean distance values one can see that the maximum distance of the clusters was gradually diminishing during the years, 84.03 ⟶ 52.14 ⟶ 41.02 in the three years, respectively. These can be explained by the environmental change of the individual stands resulted in the structural rearrangement. In this process there appeared new species of smaller or larger number in every stand and the proportion of the existing ones changed remarkably in most cases (Table 2).

It is noteworthy that a continuous increase in the number of species was observed on the examination areas during the study. The time-proportional increase of species number was larger between the second two years everywhere (Table 2).

In the subsequent analysis the relevés of the individual years were separated according to the three communities and the temporal changes in the vegetation of samples belonging to the same community were investigated one by one.

The analysis of the samples from the same periods of the three years verifies that in all the three communities such processes took place fundamentally that manifested themselves in the structural change of a similar character in the individual stands.

The group occupying the widest relief position and involving the greatest number of the sampling points represent the Potentillo-Festucetum pseudovinae community. The movement of seven points in the factorial space is demonstrated in Fig. 4. In accordance with the PCA scatter diagrams the groups of points belonging to the individual years form fairly discrete sets which means that the "behaviour" of the individual objects, namely the change in their species composition, is very similar on the individual sampling sites. In the space determined by the first three PCA axes there is no overlap among the sub-sets, therefore we may well assume that the struc-

Table 2/a

Relative plant cover at the sampling sites in the experimental years. BUGAC 05. 1981

Stands	8	1	13	2	3	5	6	7	9	10	12	4	11	14
1. Equisetum ramosissimum	9													
2. Erysimum diffusum	20													
3. Secale sylvestre	41	4												
4. Festuca vaginata	1	36	48	27										
5. Onosma arenaria				3										
6. Festuca pseudovina		8	7	31	47	40	45	63	56	46	52			
7. Eryngium campestre		6	4	8	5	15	28		1	3	4			
8. Euphorbia seguierana		6	2	12	3	7		5		1	2			
9. Carex stenophylla				3				8	5		9			
10. Potentilla arenaria			4	5	19	30	6	9	6	31	5		3	
11. Cynodon dactylon		1							5	4			6	
12. Leontodon autumnalis			1	1								1		
13. Veronica prostrata						4	12							
14. Thymus degenianus						1					2			
15. Tragopogon dubius									14					
16. Ononis spinosa								3				21	19	12
17. Molinia coerulea								3			4		25	6
18. Achillea millefolium						2	8	3	3					1
19. Galium verum					26			6		5		4	10	
20. Plantago lanceolata						1						1		1
21. Holoschoenus romanus											16		6	16
22. Poa angustifolia												62	31	24
23. Salix rosmarinifolia												4		18
24. Schoenus nigricans												6		
25. Polygala comosa														2

Table 2/b

BUGAC 05. 1985

Stands	8	1	13	2	3	5	6	7	9	10	12	4	11	14
1. Secale sylvestre	19													
2. Medicago minima	1	2	5	3			1							
3. Festuca vaginata	2	37	18	5						2				
4. Carex stenophylla	3	6	4	10	3		3	4	13					
5. Poa bulbosa	8	6	3	8	6	13			10		13			
6. Festuca pseudovina	3	12	8	31	23	20	41	29	27	46	26			
7. Eryngium campestre		1	1		1	2	1	2	1					
8. Cerastium semidecandrum	2		2	2	3	2	1	2	1		2	2		
9. Silene otites	1		1			2				1				1
10. Arenaria serpyllifolia		1	2	2	1					2				2
11. Euphorbia seguierana		1	4	1	2			7		4	1	5		
12. Potentilla arenaria		1	5	13	3	17	7	7	17	6	3		8	
13. Galium verum				1	5			5		8		18	13	3
14. Thymus degenianus			1	3	1			3		6	3			4
15. Koeleria glauca			8		1	4	14	4	7	5	6	22	8	
16. Achillea millefolium				1	11	10	7				10	9	13	
17. Stipa capillata					17	13	10							

Table 2/b (cont.)

Stands	:	8	1	13	2	3	5	6	7	9	10	12	4	11	14
18. Falcaria vulgaris	:						1			10					
19. Colchicum arenarium	:						2	2	1						
20. Euphorbia cyparissias	:					3	1	5	7				5		
21. Veronica prostrata	:					6	1	2	4	3			1		
22. Molinia coerulea	:								17			6	27	42	14
23. Calamagrostis epigeios	:													8	
24. Salix rosmarinifolia	:														19
25. Poa angustifolia	:														28
26. Ononis spinosa	:														9

Table 2/c

BUGAC 06. 1986

Stands	:	8	1	13	2	3	5	6	7	9	10	12	4	11	14
1. Medicago minima	:	1	2	1											
2. Bromus tectorum	:	2	5		1										
3. Carex stenophylla	:	3	10	2	9		4	6		10	3	2		2	
4. Eryngium campestre	:	1	3	2	1	12	11	2	4	4	1	1		6	
5. Cynodon dactylon	:	4	3	4	9		4	3	2	5	3			10	
6. Potentilla arenaria	:	1		9	1	5	15	20	6	4	16	8	1		7
7. Festuca pseudovina	:	8	16	15	18	20	15	15	14	15	21	15	15		
8. Euphorbia seguierana	:	4	1	5	1		2	1	3	3	2	6		1	1
9. Erysimum diffusum	:	2					1	2	1	1	1				
10. Festuca vaginata	:		19	18	5	3	4				2			5	
11. Dianthus pontederae	:				1		2	12			13				
12. Koeleria glauca	:			3		5	4		4	2	1	8			
13. Falcaria vulgaris	:					1	4	3		35					
14. Galium verum	:	3			5	10		2	7				6	18	2
15. Thymus degenianus	:			5	2	4	4		7	2	8	5		3	
16. Equisetum ramosissimum	:	2									1		1	1	
17. Calamagrostis epigeios	:				16	5			5		10	15	19	29	15
18. Achillea millefolium	:				3	8	6	10	6	3	2	2	5	4	
19. Silene otites	:			1		1	2	1	2			1	5	1	
20. Euphorbia cyparissias	:					5	2	3	6				2		
21. Teucrium chamaedrys	:					3		5	6				6		
22. Scabiosa ochroleuca	:					1	1	2	2				10	2	
23. Poa angustifolia	:					3		2	2	5			3	5	5
24. Plantago lanceolata	:						2						7	2	1
25. Holoschoenus romanus	:						2		2			8	2	5	12
26. Ononis spinosa	:								1			2	4	2	4
27. Carex liparicarpos	:								3				6		8
28. Schoenus nigricans	:								4				5		5
29. Salix rosmarinifolia	:														20

Fig. 5

ture of the individual stands has not remained unchanged, indicating a succession process. There is a successive increase in the distance of the weight points of sub-sets of the individual years, namely the distance is largest between the sub-sets of 1981 and that of 1986.

The same tendency applies to the samples of the other two communities, too. The samples of the three years are isolated into well-separated groups, which reflects an identical strong change of the environmental conditions in the three vegetation types.

A gradual increase in the species-cover diversity on each of the 14 sampling points is also typical. This change, accompanied with the increasing species number, also indicates the changes of the environmental conditions that have resulted in the weakening stability of the individual communities and favoured the occurrence of new species (Tables 1 and 2).

Among the groups of the objects "the most linear" change is characteristic of the samples of the Molinio-Salicetum rosmarinifoliae community. In case of samples of the Festucetum vaginatae, however, "the deviation" is not considerable. The Potentillo-Festucetum pseudovinae represents a transitional position.

Taking all these into account we must search for a factor to which the vegetation of grooves is the most sensitive.

Since among the environmental parameters the amount of the rainfall and its annual distribution fluctuate to the highest degree on the sampling area, let us compare our findings so far with the climatic changes.

Figure 6 shows the climatic changes during the last 10 years. It is characteristic of the diagram that the amounts of the rainfall reach and even exceed the average of many years till 1981 and the summer periods poor in rain is preceded by a rainfall maximum. The precipitation deficits are moderate. However, a very sharp change occurred in 1982. From that time the amount of rainfall was very low during four years, a strong precipitation deficit had developed as a consequence of the monthly amount of some mm recorded frequently.

Among others this resulted in the decrease of more metres in the water level of the soil on the sampling area, too, and the marks of draining could also be observed in the structure of the vegetation (Table 2). The unfavourable alterations in the weather conditions were also reflected in the structural transformation of the fauna. The most sensitive reactions could be seen in case of cicadas (GYÖRFFY and KÖRMÖCZI, 1987), which indicated a greater change for 1982.

KECSKEMÉT
1977
1978
1979
1980
1981
1982
1983
1984
1985
1986
°C
10.3 466
9.3 496
11.0 495
9.0 570
10.3 466
10.6 337
11.2 334
10.2 454
9.5 507
mm
30
20
10
0
120
100
80
60
40
20
0
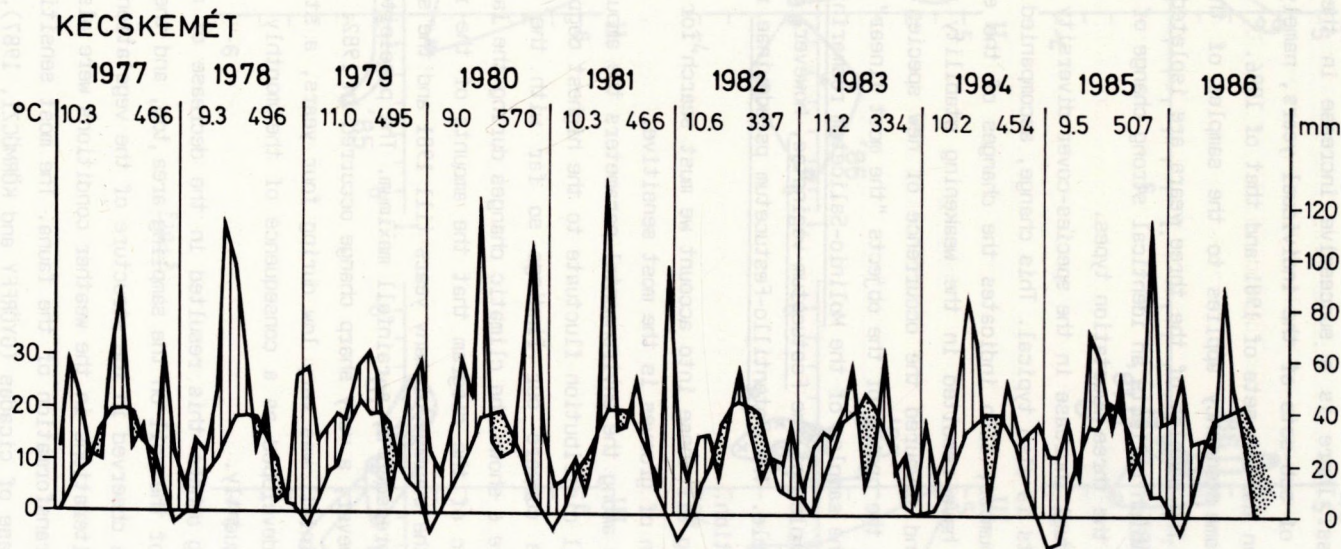
Fig. 6

It can be stated, that among the investigated communities the stands of the Molinio-Salicetum rosmarinifoliae in grooves responded to the alteration of the weather parameters with the largest structural change as they have the largest water demand on the given habitat. In periods of strong rainfall deficit their species composition came close in many respects to that of the Potentillo-Festucetum pseudovinae occupying the drier habitat. Under the influence of the given environmental alteration this community possessed the smallest stability and suffered the largest changes. It should also be noted that the stand of the sampling site No. 14 occurring on the deepest relief and supplied most favourably with water, reacted to the deterioration of conditions only with a certain lag due to its more advantageous position. Consequently, in 1985 it best resembled the sample of 1981 on the very same position and not the samples Nos 4 and 11 in the identical period. In 1986, however, it joined entirely with the two other stands of grooves.

Furthermore we can see that the successive changes in the Festucetum vaginatae are more moderate than those in the other two communities. The scattering of samples of different periods in the PCA factorial space is more moderate than that of the other two communities and the distances between the weightpoints of the groups of objects also reflect a slightly different change of condition. It can be explained by the fact that the FV stands were under less favourable conditions earlier, too. It is most likely, however, that these stands may have the largest tolerance against the changes of the weather parameters and the strongest stability under the given conditions.

In the successional changes of the PFP stands isolated from the browsing the isolation itself plays a significant role and as a consequence of it the closed grassland has become open (GALLÉ et al., 1985). The climatic changes, however, practically determine the course of the secondary succession of this community.

There remains an open question what the significance of the two different factors is as compared to each other, which of them is the primary one or the strength of their effect is changing periodically.

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Acta Botanica Hungarica 35(1-4), pp. 161-171 (1989)

ELEMENT CONCENTRATION CADASTERS IN A QUERCETUM PETRAEAE-CERRIS FOREST

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(Received: 15 May 1989)

The element content of some frequent species in a Quercetum petraeae-cerris association was investigated in the Mátra mountains, in Hungary within the scope of the ECCE-project (Element Concentration Cadasters in Ecosystems) of the IUBS. Depending on the applied investigating methods 27 and 45 elements were traceable. Species in the field layer contained the largest amounts of elements, in terms of element content per 1 g dry matter. Highest total-element content was found in calcicol and nitrophylous plants. A lower total element content was found in the species of the shrub layer and the leaves of Quercus petraea. A decreasing amount of total element content was measured in the leaves of sessile oak collected from consequent upward sections of tree crowns.

Introduction

Multi-element analysis investigations are being carried out wihtin the scope of the Element Concentration Cadasters in Ecosystems project of the International Union of Biological Sciences - organised by the Ecological Institute of Osnabruck University.

This research is aimed at determining the distribution of the elements of the periodic table in various ecosystems in the world and also measuring their natural concentrations in the soil and living organisms. A comparative data-base can be obtained in this way which can render information about accumulation of certain elements in different plants and the possible element accumulative impacts of pollutants.

Within the scope of this project investigations have been carried out in a relatively wide-ranging zonal forest community for several years.

The objective was to provide a quantitative determination of elements in the characteristic species of the forest.

Akadémiai Kiadó, Budapest

Research area

The research area was a Quercetum petraeae-cerris forest stand situated in the Mátra-mountains, North-East Mountain Region, in Hungary. The site was at an altitude of 610 m. The soil-type was lessivated brown forest soil on piroxen-andesit.

The detailed description of the soil type and floristic composition is to be found in KOVÁCS (1975).

Methods

Sampling was carried out according to the directives for multi-element analysis, i.e. MARKERT (1986) in August 1987. Samples were taken from 10 sections of each of the 10 Q. petraea crowns selected in a 150x150 m sample plot. 100 leaves were collected and mixed to one sample from each section. 10-10 samples of two species in the shrub layer, of the partial parasite Loranthus europaeus and of 9 species in the field layer were also taken.

The chemical analysis was carried out by means of ICP-AES (27 elements - in the Department of Chemistry at the Horticultural University, Budapest) and with spark source mass spectrometer (45 elements - at the Central Research Institute for Physics of the Hungarian Academy of Sciences).

Results

The following species were investigated:

Field layer: Chrysanthemum corymbosum, Convallaria majalis, Cynanchum vincetoxicum, Digitalis ambigua, Poa nemoralis, Potentilla alba, Satureja vulgaris, Serratula tinctoria, Waldsteinia geoides.

Shrub layer: Rosa canina, Rubus hirtus.

Crown layer: Quercus petraea, Loranthus europeus.

The total element content (in terms of μg element amount/100 g dry matter) showed a decrease from the field layer to the crown layer. The total element content of the leaves of field layer was 43.324-68343 μg/g (Table 1).

High amounts of the investigated elements were found in calcicol and nitrophylous plants, like Cynanchum vincetoxicum, Convallaria majalis, Digitalis ambigua, Serratula tinctoria.

Some species contained certain elements in greater quantities in their leaves as it is shown in Table 2, which was due to their selective cation uptake ability. They were as follows:

Digitalis ambigua Ca, K, Sr

Chrysanthemum corymbosum B, Cu

Convallaria majalis Ba

Cynanchum vincetoxicum Al, Mn, P, Si

Satureja vulgaris Cu

Serratula tinctoria B, Cd, Cr, Cu, K, Na, Ni

Waldsteinia geoides Al, Fe, Li, Mg, Pb, V, Zn

Two calcicolous plants (Serratula tinctoria, Waldsteinia geoides) were found to contain relatively higher amounts of microelements and heavy metals. These two can be reckoned with as potential accumulation indicating species.

Serratula tinctoria also contained the highest quantities of elements in its roots - amongst them Al, Cd, Cr, Fe, Ga, Li, Mn, Ni, Pb, Ti, V.

Some of the elements were measured in greater amounts in the roots of the investigated plants, e.g.: Al besides S. tinctoria in C. vincetoxicum, B in Ch. corymbosum and C. majalis, Ba in C. majalis, C. vincetoxicum, W. geoides. There was also a higher amount of Zn in the roots of W. geoides. Potentilla alba which thrives on mildly acidic soil had a considerable quantity of Ca.

Leaves of Rosa canina and Rubus hirtus - constituent species of the species poor shrub layer - had 31.151 - 38.916 µg/g element content (Tables 1 and 3).

The element content of the leaves of Q. petraea is lower as compared with the values of the shrub and field layers. The lower sections of the crowns contained a total of 27.899 µg/g elements, while at the top 23.818 ug/g was measured (Table 4).

By means of spark source mass spectrography 45 elements were detectable in the range of 0.01 - 1000 µg/g.

The detailed element contents of different sections are presented in Table 5. Eight elements were found in the 0.01 range at the topmost section of the crown layer. There were only 2, however, in the middle and lower sections as if indicating a drop in element concentration in the course of the upward transpirational flow. Concentration of Cd, Co, I, Pr, Sc, Y was higher in the lower sections of the crowns. Au and U were also detectable in the inferior layers.

Smaller amounts of Ca, Mg, K, Na were found in the samples taken from the upper sections. Thus the reduced buffer capacity of these laeves may result in less tolerance of acidic air pollutants, either in the form of dry or wet deposition.

Table 1

Total element content of the species in a Quercetum petraeae-cerris forest stand (μg/g)

	root	stem	leaf
Chrysanthemum corymbosum	31941	25910	55246
Convallaria majalis	18464	71394	57790
Cynanchum vincetoxicum	31240	23307	59070
Digitalis ambigua	32519	37339	68343
Poa nemoralis	-	14941	
Potentilla alba	31097	44418	43324
Satureja vulgaris	20282	25783	43358
Serratula tinctoria	43657	40912	65612
Waldsteinia geoides	30606	-	51005
Rosa canina	-	22143	31151
Rubus hirtus	-	16015	38917
Loranthus europaeus	-	17576	57863

Table 2

Element content of some frequent species in the field-layer of Quercetum petraeae-cerris association (μg/g)

		A	B	C
Element	Plant	root	stem	leaf
Al	1	1176	21.9	157.0
	2[x]	2153	182.7	144.5
	3	5656	42.4	408.6
	4	1026	41.3	125.1
	5[xx]	-	67.3	
	6	724.8	73.7	201.6
	7	882	68.4	295.2
	8	15011	71.2	222.6
	9	3894	-	671.9
B	1	18.6	10.9	74.4
	2	18.4	16.9	22.3
	3	6.0	11.7	26.8
	4	15.0	13.0	16.3
	5		0.7	
	6	17.3	28.7	34.6
	7	8.7	16.5	36.3

		A	B	C
Element	Plant	root	stem	leaf
B	8	ny	20.3	54.0
	9	16.8	-	45.7
Ba	1	75.4	33.4	32.1
	2	124.0	170.4	104.8
	3	103.3	41.4	39.7
	4	87.8	54.7	55.1
	5		-	28.6
	6	91.7	99.2	33
	7	54.1	113.4	57.4
	8	87.2	57.2	43.6
	9	104.2	-	63.6
Ca	1	8578	3251	11414
	2	5283	7993	16315
	3	8116	5774	16701
	4	11162	6007	21370

Table 2 (cont.)

		A	B	C
Element	Plant	root	stem	leaf
Ca	5	–	1893	
	6	19440	7262	13249
	7	4192	5974	14391
	8	6321	6078	16449
	9	9200	–	16562
Cd	1	2.5	1.2	1.4
	2	1.3	1.5	0.6
	3	0.9	0.5	0.6
	4	–	0.2	
	5	–	–	–
	6	1.6	0.7	0.3
	7	0.3	0	0
	8	2.2	2.1	1.5
	9	1.3	–	0.9
Co	1	0.7	0	0
	2	1.0	0	0
	3	1.5	0	0
	4	0.6	0	0
	5	–	0	
	6	0	0	0
	7	0.4	0	0
	8	5.8	0.3	0
	9	1.2	–	0
Cr	1	0.8	0	0.5
	2	1.2	0	0.5
	3	1.2	0	0
	4	1.7	0	0
	5	–	0	
	6	0.8	0	0
	7	ny	0	1.2
	8	4.5	1.3	2.2
	9	2.7	–	0.9
Cu	1	11.7	2.5	7.7
	2	9.4	2.7	2.6
	3	6.3	4.7	6.4
	4	16.6	4.2	3.6
	5	–	2.8	
	6	8.0	8.0	5.2
	7	12.5	3.9	7.1
	8	12	4.9	7.9
	9	9.8	–	5.6
Fe	1	822.9	43.9	209.4
	2	1304	149.2	167.0
	3	3359	48.9	371.5
	4	592.1	72.1	147.5

		A	B	C
Element	Plant	root	stem	leaf
Fe	5	–	182.6	
	6	350.5	158.2	190.4
	7	529.4	82.1	319.6
	8	10341	136.1	364.8
	9	2456	–	551.8
Ga	1	2.9	0	0
	2	0	0	0
	3	5.6	0	0
	4	0	0	0
	5	–	0	
	6	0	0	0
	7	2.7	0	0
	8	17.9	0	0
	9	4.2	0	0
K	1	17388	21082	38854
	2	8478	58390	34067
	3	9719	20666	34122
	4	13960	28395	40309
	5	–	11561	
	6	5568	33840	24040
	7	11085	16781	23023
	8	7745	31692	41397
	9	8910	–	23033
Li	1	0.6	0	0.5
	2	0.6	0	0
	3	2.1	0	0
	4	0.5	0	0
	5	–	0	
	6	0.3	0	0.2
	7	0.4	0	0
	8	6.4	0	0.2
	9	1.6	–	2.8
Mg	1	1555	595	2634
	2	1306	1806	3863
	3	2033	1347	3594
	4	2918	1307	4241
	5	–	651	
	6	2590	1230	3259
	7	1810	1293	5170
	8	1590	1343	4952
	9	3238	–	7580
Mn	1	428.7	58.3	195.7
	2	223.5	106.3	214.6
	3	459.8	141.0	452.7
	4	342.4	60.8	69.7

Table 2 (cont.)

Element	Plant	A root	B stem		C leaf
Mn	5	-		53.4	
	6	210.3	123.4	53.4	215.5
	7	107.1	49.8		105.9
	8	764.9	174.9		227.3
	9	487.9	-		277.5
Na	1	187.4	140.9		159.6
	2	165.5	160.2		144.2
	3	183.1	161.6		163.0
	4	174.4	139.4		164.9
	5	-		1205	
	6	141.8	141.4		152.8
	7	147.2	134.8		136.6
	8	241.3	163.5		174.9
	9	146.1	-		147.4
Ni	1	1.3	0		0
	2	1.3	0.6		0.7
	3	1.2	1.1		0.7
	4	2.9	ny		1.1
	5	-		0.6	
	6	0.7	ny		0.4
	7	0.7	0		1.6
	8	4.4	3.8		3.6
	9	2.6	-		0.4
P	1	1247	556.4		1263
	2	1581	2103		2481
	3	1289	2136		2820
	4	1868	1113		1534
	5	-		1454	
	6	1455	1266		1662
	7	1077	1108		1488
	8	915.4	1057		1445
	9	1777	-		1651
Pb	1	8.2	0		3.8
	2	3.5	0		0
	3	5.9	0		0
	4	8.1	0		0
	5	-		0	
	6	4.2	0		0
	7	3.1	0		3.2
	8	19.4	0		0
	9	7.6	-		4.2
Se	1	0	0		0
	2	0	0		0
	3	0	5.3		0
	4	0	0		0

Element	Plant	A root	B stem		C leaf
Se	5	-		0	-
	6	0	0		0
	7	0	0		0
	8	0	0		0
	9	0	0		0
Si	1	-	68.2		142.5
	2	149.7	189.4		175.3
	3	107.3	63.5		240.6
	4	210.5	74.3		191.9
	5	-		185.5	
	6	259.3	97.9		212.9
	7	304.7	90.5		205.8
	8	122.5	126.0		145.6
	9	116.6	-		228.5
Sr	1	44.3	25.6		38.3
	2	25.7	46.9		61.2
	3	40.8	30.7		44.0
	4	62.0	43.6		86.2
	5	-		7.3	
	6	104.8	56.8		41.4
	7	20.3	36.9		42.8
	8	42.1	47.1		65.9
	9	49.2	-		58.4
Ti	1	22.8	0.3		2.9
	2	31.7	2.3		1.8
	3	85.9	0		5.0
	4	7.5	0.4		1.7
	5	-		1.5	
	6	3.4	1.1		2.5
	7	13.7	1.1		5.3
	8	231.9	1.4		3.5
	9	62.9	-		12
V	1	2.4	0		0.4
	2	2.9	0.3		0.3
	3	7.0	0		0.6
	4	1.7	0.3		0.3
	5	-		0.2	
	6	1.2	0.2		0.4
	7	1.4	0		0.5
	8	22.1	0.4		0.3
	9	5.5			1.0
Zn	1	60.3	18.5		54.8
	2	66.5	73.5	24.0	
	3	50.3	41.8		72.8
	4	60.9	13.2		25.5

Table 2 (cont.)

Element	Plant	A root	B stem	C leaf
Zn	5	-	31.1	
	6	123.4	29.9	23.4
	7	29.4	30.2	67.6
	8	65.9	34.9	52.4
	9	110.8	-	101.9

1. Chrysanthemum vulgare
2. Convallaria majalis x)
3. Cynanchum vincetoxicum
4. Digitalis ambigua
5. Poa nemoralis xx)
6. Potentilla alba
7. Satureja vulgaris
8. Serratula tinctoria
9. Waldsteinia geoides

Data of As, Hg, and Mo are not presented, because none of the samples contained them in measurable amounts.

x) whole stolons were analysed
xx) stem and leaf were not separated

Table 3

Element content of different parts of Rosa canina (1) and Rubus hirtus (2) (μg/g)

	1 stem	1 leaf	2 stem	2 leaf
Al	51.4	181.1	23.3	119.9
As	0	0	0	0
B	16.8	59.7	9	35
Ba	41.8	30.5	31.9	48.4
Ca	8169	12122	3551	13300
Cd	0	0.2	0.2	0
Co	0	0	0	0
Cr	9	1.8	0.9	2.1
Cu	5.6	4.2	0.5	5.4
Fe	65	200.6	89.3	176.5
Ga	0	0	0	0
Hg	0	0	0	0
K	10556	13479	9125	17477
Li	0	0.2	0	0
Mg	1639	2886	1244	4361
Mn	102.9	265.1	60.8	329.2
Mo	0	0	0	0
Na	182.7	140.3	136.3	152.7
Ni	1.1	1.1	1.1	0

Table 3 (cont.)

	1		2	
	stem	leaf	stem	leaf
P	1160	1679	1626	2739
Pb	0	3.4	0	0
Se	0	4.5	0	0
Si	75.5	47.7	58.4	74.2
Sr	51.7	46.9	26.5	59.2
Ti	0	2.1	0	1.6
V	0	0.4	0	0.3
Zn	25.3	15.6	30.8	36.1
	Σ 22143.8	31151.4	16015	38917.7

Leaves of the epiphyte Loranthus europeus contained more than twice the amount of elements contained by Q. petraea leaves (57.683 μg/g) (Table 6). The Ca, Mg, P, K contents were also higher than in Q. petraea.

Summary

The total element content (in μg element/g dry matter) of the investigated plants was found to decrease from the field layer to the crown layer in the Quercetum petraeae-cerris association.

The calcicol and nitrophylous plants in the field layer were characterised by high element content.

The obligatory calcicolous species (S. tinctoria, W. geoides) contained relatively high amounts of heavy metals in their organs, too.

Total element content (e.g.: Ca, Mg, K, Na) in the crowns of Q. petraea decreased from the inferior parts to the top. Several elements were measured in a mere 0.01 μg/g amount in the upper parts. Au and U were traceable only in the lower sections.

Table 4

Element content in the leaves of Sessile oak (*Quercus petraea*) in Mátraháza
Samples were taken from different layers of the tree crowns: 1) highest layer; 10 lowest layer
(μg/g - mean value of 100 leaves in each layer)

Element	1	2	3	4	5	6	7	8	6	10
Al	59.1	57.6	60.4	62.2	59.2	66.4	67.2	74.4	68	97.3
As	0	0	0	0	0	0	0	0	0.3	0
B	23.2	19	21.2	24.7	24.1	23.7	25.5	21.6	22.1	29.3
Ba	70.1	67.8	69.6	75.7	75.2	73.1	71.4	67.7	69	82.9
Ca	9467.6	9391	9545.4	9921.4	9382.2	9051	9424.4	9018.3	9202.4	10274.6
Cd	0.02	0	0.06	0	0.02	0.04	0.1	0.05	0.02	0.02
Co	0.04	0.03	0.08	0.1	0.03	0.09	0.1	0.08	0.08	0.1
Cr	0.1	0.1	0.2	0.2	0	0.07	0.2	0.1	0.2	0.2
Cu	5.4	5.1	5.5	5.3	5.3	5.8	5.5	5.6	6.7	6
Fe	128.6	107.3	121.6	121.2	129.2	188.4	121.4	130	121.4	149.9
Ga	0.9	0.05	0.6	1	0.3	0.8	0.6	0.5	1	1.1
Hg	0	0	0	0	0	0	0	0	0	0
K	10038.9	10056.1	10973.9	11218.1	11421.9	11365.1	11535.8	11649	11853.5	12426.9
Li	0.02	0.02	0.09	0.05	0.03	0.02	0.1	0	0	0.02
Mg	1444.7	1516.9	1591.3	1654.7	1699.4	1735.7	1743.4	1711	1732.6	1813.9
Mn	603.6	709.9	674.4	725.7	694.5	622.7	705.1	762.4	704.9	704.6
Mo	0	0.04	0.08	0.04	0.05	0.07	0.04	0.03	0	0
Na	108	94.2	103.1	116.2	109.6	106.1	104.3	111.5	103.9	116.5
Ni	0.2	0.1	0.4	0.4	0.4	0.2	0.2	0.3	0.5	0.5
P	1670.6	1677	1814	1795.8	1874.6	1832.2	1921.9	1720.3	1797.9	1988.1
Pb	0.7	0	0.4	0.3	0	0	0	0	0.3	0.7
Se	0.4	0	0.5	0.4	0.6	0	0.4	0.6	0	0
Si	152.6	166.6	157.3	146.6	162.6	161.4	151.5	157.7	146.7	158.4
Sr	20.6	20.5	21.3	23.3	20.9	20.4	21.2	20.4	21.3	24.5
Ti	0.9	0.7	0.8	0.7	0.8	0.9	0.9	1.2	0.9	1.4
V	0.02	0	0.1	0	0.03	0.02	0.07	0.1	0	0.1
Zn	21.7	18.1	22.6	20	20.8	20.4	20.3	19.4	21.6	22.6
Total amount	23818	23908	25184	25914.09	25681	25273	25920	25471	25875	27899

Table 5

Element concentration cadastre of Quercus petraea leaves in the upper, middle and lower layers of the tree crowns (Data based upon spark-source mass spectrometer measurements carried out in the Central Research Institute for Physics of the Hungarian Academy of Sciences)

Element content (μg/g)	0.01	0.1		1	10	100	1000
Upper layer	Cd	As	Mo	B	Al	Cl	Ca
	Co	Ag	Nd	Na	Ba	Fe	N
	Cs	Br	Sb	Ni	Cu	K	Si
	I	Ce	V	Pb	Sn	Mg	
	Nb	Cr	Zr	Rb	Sr	Mn	
	Pr	F		Ti	Zn	P	
	Sc	Ga				S	
	Y	La					
Middle layer	Cs	As	Nd	B	Al	Fe	Ca
	Nb	Ag	Mo	F	Ba	K	N
		Br	Pr	Ni	Cl	Mg	Si
		Cd	Sb	Pb	Cu	Mn	
		Ce	Sc	Rb	Na	P	
		Cr	Th	Ti	Sn	S	
		Co	V		Sr		
		Ga	Zr		Zn		
		I					
		La					
Lower Layer	Cs	Ag	U	As	Al	Cl	Ca
	Nb	Au	V	B	Ba	Fe	K
		Cd	Y	Br	Cu	Mg	N
		Ce	Zr	Cr	Na	Mn	Si
		Co		F	Ni	P	
		I		Ga	Sn	S	
		La		Sr	Zn		
		Mo		Rb			
		Pr		Ti			
		Sb					

Table 6

Element content of the leaves of Loranthus europaeus in Mátraháza (µg/g)

Element	Stem	Leaf
Al	76.6	55.4
As	0	0
B	49.3	17.4
Ba	122.5	71.7
Ca	14691	4372
Cd	0.2	0.5
Co	0	0
Cr	0	0.6
Cu	9.8	9.4
Fe	150.1	147.8
Ga	0	0
K	36334	9789
Li	0	0
Mg	2133	1135
Mn	1527	191.5
Mo	0	0
Na	166.2	148.1
Ni	0.9	0.3
P	2489	1519
Pb	0	5.1
Se	0	0
Si	52.4	61.1
Sr	37.2	18.7
Ti	0.5	0.7
V	0	0.4
Zn	23.7	32.8
	57863	17576

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Acta Botanica Hungarica 35(1-4), pp. 173-184 (1989)

COMPARATIVE HISTOLOGICAL STUDY OF DISEASED AND SOUND QUERCUS PETRAEA STEMS

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(Received: 15 November 1987)

The paper gives account of the results of the author's examinations of some factors (reduced water transporting- and respiration capacity) which take part in the disease process/destruction of Quercus petraea, involving anatomical changes.

Introduction

There are several factors possibly responsible for the destruction of trees - first of all of sessile oak (Quercus petraea (Matuschka)Lieblein) - in the oak forests of Hungary. Those competent in the question are not of the same opinion either in Hungary or abroad, as yet. Unfortunately, very few concrete data are available at present on the abiotic and biotic factors causing the destruction of sessile oak trees and on the action mechanism of these factors (BABOS et al., 1985; IGMÁNDY et al., 1984; JAKUCS, 1984; JAKUCS and TÓTH, 1984).

The paper contains the results of examinations aimed at determining the widths of annual rings in sound and diseased sessile oak trees, the number and size of tracheae in green shoots, and the number and size of the stomata of leaves.

Material and Method

For the purpose of examination diseased and dry as well as sound stems and excised stem parts were collected in 1984-1986 from two growing sites: the forest areas Piliscsaba 3 B and Sajóbábony-Parasznya 66 A. Furthermore, from sound and diseased sessile oak trees of the two growing sites one-year old shoots from the lower part of the crown were collected for histological examinations, and leaves similarly from the base of the crown - so-called light-leaves - for stoma examinations.

To establish the course of the disease we measured the widths of the annual rings (and the spring- and autumn timber within), and followed in four directions their changes over a shorter-(10 years) and a longer (46 years) period preceding felling. The annual values of growth-ring widths measured by microscope then averaged were plotted diagrammatically.

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The green shoots were collected from the trees marked out at the same date of the vegetation period. This point of time followed the first growth phase. The green shoots collected included the first and second internode below the terminal bud. For the histological examinations the material was taken from the second internode following the terminal bud of each shoot. The samples were dehyrated, imbedded in paraffine; then cross-sections were prepared from them and stained. On the whole cross-section surface of the preparations microscope measuring was carried out, and the tracheae found there were counted. For each tree 3 parallel green shoots were used in the examination. The values obtained were averaged and tabulated. To make the results of the histological examination more expressive microscope photographs were taken of the preparations.

For the stoma examinations leaves of identical position were taken from the same trees on two occasions (16 June and 28 August) in the same vegetation period. The leaves were cleaned, then stained, and the preparations thus made were subjected to microscope measuring. On both collecting dates we worked with 3 parallel leaves for each tree. On the lower epidermis of the leaves the stomata were counted on 3x3 cm^2, and the measurements of 100 stomata were taken. The averages of the data obtained are shown in a table.

Results

Annual ring width

Average annual ring widths of the last 10 years of diseased and sound stems from two growing sites, together with the precipitation data were plotted diagrammically (Figs 1, 2). As seen in Fig. 1, the annual ring width values for the diseased stems decrease, while those for the sound ones increase. Figure 2 shows a similar decrease in the annual ring widths of the diseased stems and increase in those of the sound ones. The varying average annual ring widths of the diseased and sound stems did not show correlation with either the annual precipitation data or those in the vegetation period (March-October). As regards the 10 years' average of annual precipitation and of precipitation in the vegetation period there is hardly any difference between the two growing sites (Sajóbábony 1975-1984 = = 560.3 mm and 434.1 mm; Piliscsaba 1974-1983 = 570.3 and 424.6 mm, respectively).

The average annual ring widths of the stems examined are contained in Table 1. The data of the table confirm what the diagrams show. The values for the sound stems of Piliscsaba and Sajóbábony (1215.8 and 2457.5 µm = 100%) are much higher than those for the diseased ones (790.7 µm = 65.05% and 1822.5 µm = 74.17%).

With diseased and sound stems from Piliscsaba a longer period (46 years) was also examined for changes in annual ring width. The annual ring width averages of the last 46 years of these stems were also plotted diagrammatically (Fig. 3). As seen in Fig. 3, the annual ring width values for
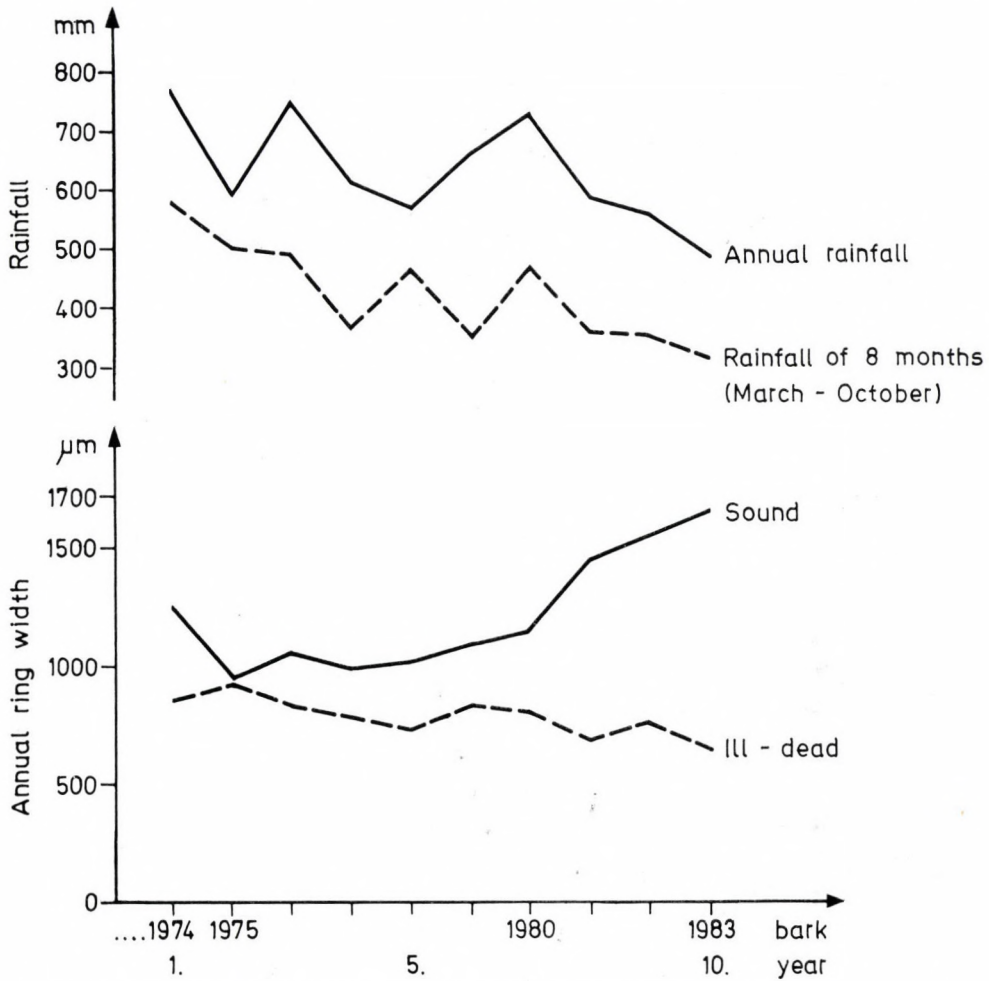
Fig. 1. The average values of the annual ring width measured at the breast height (1.3 m) of three ill and three sound Q. petraea stems in the last 10 years and the values of the rainfall (provenance: Piliscsaba, 1985)
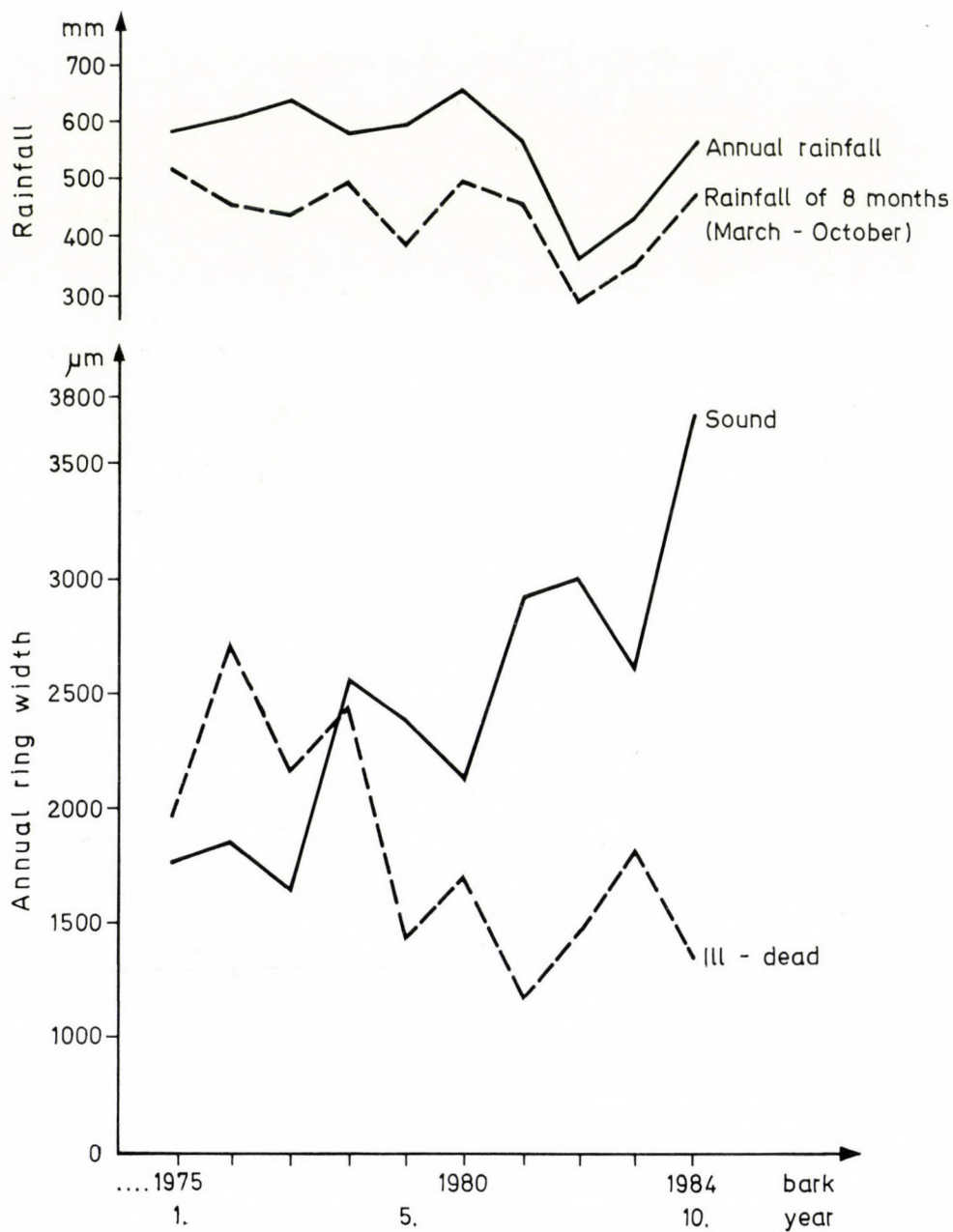
Fig. 2. The average values of the annual ring width measured at the breast height (1.3 m) of two ill and sound Q. petraea stems in the last 10 years and the values of the rainfall (provenance: Sajóbábony, 1985)

Table 1

The average annual ring width values of the ill and sound Quercus petraea stems, measured in the last 10 years

Denomination	Annual ring width early-wood late-wood µm
I. Quercus petraea - sound Mean of three stems	1215.8 = 100% 731.6 484.2 Proportion of wood = 1.51
II. Quercus petraea - sound Mean of two stems	2457.5 = 100% 1007.5 1450.0 Proportion of wood = 0.69
I. Quercus petraea - ill Mean of three stems	790.7 = 65.05% 460.4 330.3 Proportion of wood = 1.56
II. Quercus petraea - ill Mean of two stems	1822.5 = 74.17% 760.0 1062.5 Proportion of wood = 0.71

Note: Origin of I: Piliscsaba 3 B forest area-Pilis mountain, 342 m, sea-level altitude, eastern slope, age of the tested stems: 71-72-75 years; coppice, collected in 1985.

Origin of II: Sajóbábony 66 A forest area-Bükk mountain, 325 m, sea-level altitude, northern slope; age of the tested stems: 112 years, origin: seedling; collected in 1985.

the diseased and sound stems ran parallel between 1939 and 1970, moreover, later in that period the values for the diseased and destroyed stems were higher than those for the sound ones. From 1971 to 1984 the values for the latter were higher and increased, while those for the diseased stems were lower and showed a decreasing tendency. The average values for the stems examined are contained in Table 2. The data of the table confirm what the diagrams show. The annual ring widths of the diseased and sound stems when averaged over 32 years (1939-1970) show a difference, with those of the diseased ones being higher (936.77 µm) compared to 862.71 µm for the sound stems. Even in the 14-year period (1957-1970) preceding the disease the average annual ring widths of the stems later getting diseased were higher
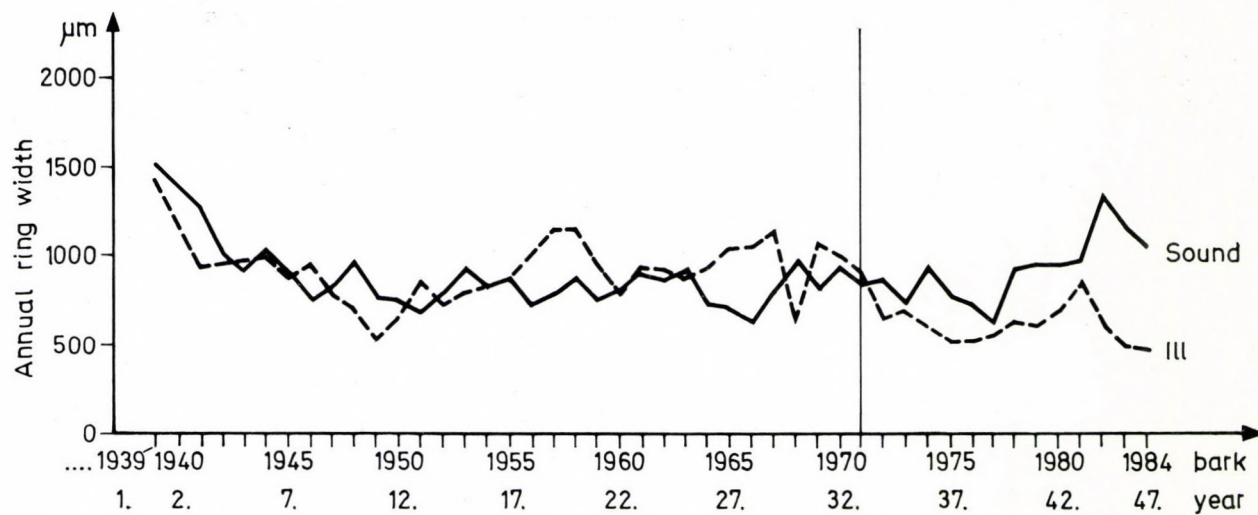
Fig. 3. The average values of the annual ring width measured at the breast height (1.3 m) of ill and sound *Q. petraea* stem in the last 46 years (provenance: Piliscsaba, 1986)

Table 2

The average annual ring width values measured in the ill and sound stems of Quercus petraea in the last 46 years, in several breakings down

(Provenance: Piliscsaba 3 B, 1986)

Denomination	Annual ring width early-wood late-wood µm
Quercus petraea - sound	862.71
Mean of two stems	601.78
1939-1970 = 32 years	260.93
	Proportion of wood = 2.30
Quercus petraea - ill	936.77
Mean of two stems	597.65
1939-1970 = 32 years	339.12
	Proportion of wood = 1.76
Quercus petraea - sound	823.20 = 100%
Mean of two stems	561.60
1957-1970 = 14 years	261.60
	Proportion of wood = 2.14
Quercus petraea - sound	980.76 = 119.13%
Mean of two stems	666.34
1971-1984 = 14 years	314.42
	Proportion of wood = 2.11
Quercus petraea - ill	973.35 = 100%
Mean of two stems	635.64
1957-1970 = 14 years	337.64
	Proportion of wood = 1.88
Quercus petraea - ill	685.38 = 70.42%
Mean of two stems	414.42
1971-1984 = 14 years	270.96
	Proportion of wood = 1.52

Note: The sound stems are 75-76 years old. The ill stems are 75-77 years old.

(973.35 μm = 100%) than those of the sound ones (823.20 μm = 100%). In the last 14 years (1971-1984) on the other hand, the annual ring widths of the sound stems gave the higher average value (980.76 μm = 119.13%) compared to 685.38 μm (70.42%) for the diseased stems.

The average values of early wood and late wood contained in Table 2, as well as the wood ratios (between 1971 and 1984) calculated from them show that the proportion of early wood within the annual ring (large tracheae = higher water transporting capacity) is higher in sound than in diseased stems. The higher proportion when expressed in percentage gives the following result: in diseased stems the early wood (414.42 μm = 60.46%) is only 20.93% wider than the late wood (270.96 μm = 39.53%), while in the case of sound stems the former (666.34 μm = 67.94%) is wider by 34.89% than the latter (314.42 μm = 32.05%), if the annual ring width is taken for 100%.

According to the results of annual ring width examinations we have succeeded in exposing a process of destruction (course of disease) of oak-trees which takes a shorter (6.8 years) or longer (13 years) time of the life of the tree. This process is clearly shown by the decreasing value of the annual ring width, and within it the narrower early wood (reduced water transporting capacity).

Size and number of tracheae in green (lignifying) shoots

In microscopic cross-sections of green shoots we counted the tracheae in the xylem just forming a closed ring, and measured the tangential and radial diameters of the tracheae. The measuring results are contained in Table 3. According to the data of the table, in the sound stems of both growing sites the cambium produces more tracheae (100%) than in the diseased stems. For example in the cross-sections of green shoots from the diseased stems the number of tracheae is only 62.81% and 64.12%, respectively, compared to that in the sound stems. In the sound stems somewhat larger tracheae were formed than in stems at the beginning of and during the disease (see Table 3 and Figs 4-5). It should be noted, however, that the tracheae showed but minimum differences in size.

Number and size of stomata

The measurements of stomata to be found on the lower epidermis of foliage leaves, and the number of stomata per unit surface are contained in Table 4. According to the data of the table the stomata in the epidermis

Table 3

Average number and sizes of tracheae in the green shoots of the Quercus petraea stems of different health condition

Denomination	Sound stem: Trach. rad.	Sound stem: Trach. tang. diameter, µm	Sound stem: Trach. number	Incipient illness of the stem: Trach. rad.	Incipient illness of the stem: Trach. tang. diameter, µm	Incipient illness of the stem: Trach. number	Ill stem: Trach. rad.	Ill stem: Trach. tang. diameter, µm	Ill stem: Trach. number
Provenance: Sajóbábony 3B, 29.05.1986									
Minimum	9.30	9.30		9.30	9.30		9.30	9.30	
Mean	19.01	14.19	134.28	20.88	16.37	91.80	21.40	15.64	86.09
Maximum	41.85	23.25	100%	46.50	37.20	68.37%	41.85	37.20	64.12%
Provenance: Piliscsaba 66A, 16.06.1986.									
Minimum	9.30	9.30		9.30	9.30		9.30	9.30	
Mean	23.00	14.71	139.20	21.04	14.55	91.91	24.14	15.52	87.43
Maximum	46.50	37.21	100%	37.20	32.55	66.03%	41.85	32.55	62.81%
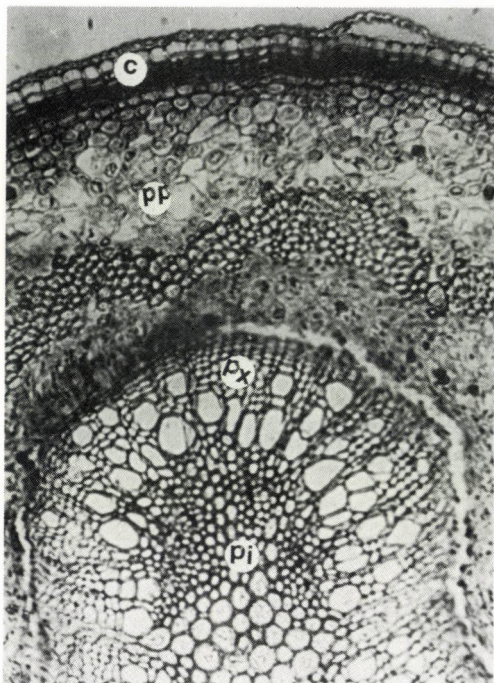
Fig. 4. Detail of the cross-section of a sound Q. petraea green shoot. Microphotograph: 120x. (Piliscsaba-39 tree, 1986). pi=pith, px=primary xylem, pp=primary phloem, c= cortex
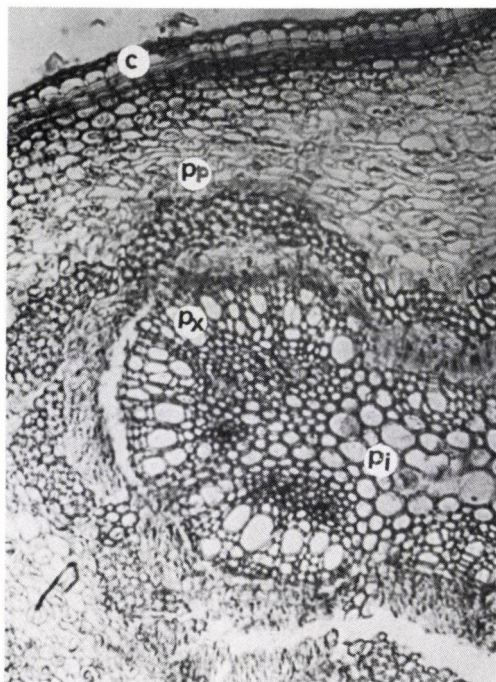
Fig. 5. Detail of the cross-section of an ill Q.petraea green shoot. Microphotograph: 120x. (Piliscsaba-198 tree, 1986). pi=pith, px= primary xylem, pp=primary phloem, c=cortex

Table 4

Sizes and number of the stomata on the light-leaves of the ill and sound Quercus petraea stems (Origin: Piliscsaba 3B, 1984, 1985; Sajóbábony 66A, 1984, 1985)

Origin	Size of stoma µm Minimum - Mean - Maximum	Number of the stomata/cm² Mean
Sajóbábony, 1984-sound stem light-leaf in the lower position	length 18.72 - 25.23 - 31.74 100%	
	width 12.46 - 16.65 - 23.40 100%	
Sajóbábony, 1984 - ill stem light-leaf in the lower position	length 12.48 - 17.43 - 21.48 69.08%	
	width 9.36 - 14.49 - 20.28 87.02%	
Sajóbábony, 1985 light-leaf in the lower position	-	sound = 347.4 - 100% ill = 274.4 - 78.98%
Piliscsaba, 1985 light-leaf in the lower position	-	sound = 324.8 - 100% ill = 281.3 - 86.60%
Piliscsaba, 1986 light-leaf in the lower position	-	sound = 398.0 - 100% ill = 316.6 - 79.54%

of leaves from sound stems are larger in size and higher in number per unit surface than in the case of diseased stems. So, the length of stoma for diseased stems is only 69.08% and its width 87.02% of the corresponding stoma measurements for sound stems; further, the number of stomata per unit surface of leaves from diseased stems is only 78.98-86.60% compared to sound stems.

The lower number and smaller size of stomata obtained for the diseased stems mean a reduced respiration capacity.

Summary

On the basis of the results of examinations carried out so far it can be established that the course of the disease of Quercus petraea s.l. in question takes a shorter (6-8 years) or longer (13 years) time of the life of the tree and leads to its complete destruction.

This process, the disorder of the physiological functions of diseased trees is clearly indicated by

- the decreasing value of the annual ring width,
- the reduced water transporting capacity attributable to the narrower spring timber and
- to the lower number of tracheae in the green (lignifying) shoots,
- the reduced capacity of the respiratory apparatus in the lower epidermis of foliage leaves (in the leaves of diseased trees the number and size of stomata are smaller).

To sum it all up, from a histological point of view the following phases can be established in the process of Quercus petraea destruction: set-in of the disease ⟶ decreasing width of annual ring (and narrower early wood within it) ⟶ fewer tracheae formed in the green (lignifying) shoots ⟶ fewer and smaller stomata per unit surface of leaf.

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Acta Botanica Hungarica 35(1-4), pp. 185-198 (1989)

EFFECT OF HEAVY METALS INHIBITING THE GROWTH OF PLANT CALLUS TISSUES (III)

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(Received: 22 March 1988)

The authors studied the effects of various concentrations of six heavy metals on the growth of secondary callus tissue cultures of Ruta graveolens L. The experiments were aimed at determining the limits of tolerance shown by the cell population of rue to the compounds applied and to their divalent metal ions, respectively. The following ions were put to test: cadmium (Cd), copper (Cu), mercury (Hg), nickel (Ni), lead (Pb) and zinc (Zn). The concentrations ranged between 10^{-4} and 10^{-6} M, or from 10^{-5} to 10^{-7} M in the case of mercury. The incubation culture medium contained WHITE's macroelements (1954) completed with HOAGLAND's microelements and with 6 mg 2,4-D and 4 mg IAA per litre. The incubation lasted 4 weeks at a temperature of 25 ($\pm$2) ^{o}C with 16-hour light and 8-hour dark periods. The rate of illumination was 120 W/m^2. The effect of the heavy metals used in the experiments was characterized by the change in the fresh and dry weight of the callus tissue and in the number of cells per units weight.

As seen from the results of the experiments the effect of the metal ions and compounds was a function of the concentration; nevertheless, any concentration applied inhibited the growth of the fresh weight of rue callus. In comparison to the control it was inhibited most by copper and least by lead and mercury, and the highest concentrations of nickel and copper evan caused lethality. The dry weight increased in inverse ratio to the inhibition of fresh weight, due to the dehydration of the cells, a sign of the toxicity of heavy metals. The number of cells varied, often it was the same as in the control. As shown by the experiments the toxicity of heavy metals may manifest itself in the dehydration of cells. Further, the results obtained indicate that the limit of tolerance to toxic heavy metals may vary with the plant species, it is therefore desirable to carry out screening with as many species as possible (MARÓTI and BOGNÁR, 1985).

Introduction

The pollution of our environment can no longer be stopped, only moderated, if at all (BELL, 1980; DÄSSLER, 1979; KOVÁCS, 1975, 1985). We must therefore size up the possibilities, e.g. in respect of the toxic heavy metals. The first step might be to acquire a knowledge of the tolerance or resistance of plants to various concentrations of these metals (HORVÁTH, 1983; KOVÁCS et al., 1986; WALLACE, 1977).

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The relevant literature and our own experiments suggest that there are great difference in the uptake of various toxic heavy metals between the plant species according to their genetic and physiological conditions (DIJKSHOORN et al., 1979; MARÓTI and BOGNÁR, 1985, 1988; PAIS, 1980; WALLACE, 1977).

The toxicity of heavy metals should be known first of all with a view to the health of those (people and animals) consuming the plants. The evaluation of data collected of various plant species by exáct reproducible tissue cultures is also necessary. This purpose is served by the results published below of the experiment series started by us.

Materials and Method

Ruta graveolens L., the plant used in our experiment is known as a medicinal plant, too. A so-called secondary callus culture cultured for several years was our test material. The cell population of callus has a moderate intensity of growth and gives special organization responses to the known regulators (MARÓTI and DÉKÁNY, 1977; MARÓTI et al., 1972).

The cultures were incubated in a modified culture medium of WHITE (1954) completed with HOAGLAND (A-Z) solution and with 6 mg di-chloro-phenoxy-acetic acid (2,4-D) and 4 mg indole-acetic acid (IAA) per litre. The culture medium was sterilized in autoclave. The incubation period was 4 weeks. The cultures were kept at 25(±2) ^{o}C with 16/8 L/D periods. The rate of illumination was 120 W/m^2 (MARÓTI and BOGNÁR, 1985; MARÓTI and DÉKÁNY, 1977).

The heavy metals examined were: cadmium ($Cd(CH_3COO)_2$), copper ($CuSO_4$), mercury ($HgCl_2$), nickel ($NiSO_4$), lead ($Pb(NO_2)_2$), zinc ($ZnSO_4$), in the form of the compounds indicated. The concentrations applied ranged between 10^{-4} and 10^{-6} M, except the concentration of mercury which varied between 10^{-5} and 10^{-7} M (MARÓTI and BOGNÁR, 1985, 1988).

From the callus tissue of rue 200 mg was placed onto 25 ml culture medium containing agar-agar. Each variant consisted of 10 flasks with three replications. To check up the effect of the metals we took the fresh and dry weight and the cell number every day, and recorded the daily and relative changes of these parameters. Both the seatter of the measured data and their percentage values compared to the control are given (MARÓTI, 1976; THOMAS and DEWEY, 1975).

Acknowledgements

The authors are indebted to Miss E. LÉH and Mrs. G. HALMAI for their technical assistance during the experiments.

Results and Discussion

The measured and converted data are shown in Tables (1-6) and Figures (1-6).

The concentrations of the heavy metals had highly varying effects on the growth morphology of the callus tissue cultures. This statement is well perceptible when the effects of these compounds are considered as a function of the changes in the three parameters (fresh weight, dry weight, cell number). It would seen natural that with higher concentrations - i.e. increasing toxicity - the values of the metabolic indices decrease, as proved by the fresh weight data, too. However, the percentage proportion of dry weight and the number of cells per unit weight of callus show opposing tendencies; and they either show the tendency of the values obtained in the control, or even increase with an increase in the concentrations. The only exception is mercury under the influence of which the changes in all three parameters show the same tendency, and an increase in concentration increase the inhibition.

Fresh weight increase was most inhibited by copper (57-90 per cent), and least by lead (8-49 per cent) and mercury (7-36 per cent). Under the influence of zinc, cadmium and lead the proportion of dry weight was 1-23 per cent lower, while in response to mercury, nickel and copper 1-24 per cent higher than in the control. With zinc and mercury applied the number of cells per g of callus - similarly to the change of fresh weight - decreased with an increase in concentration, while the other metals act on it the same way as in the control or caused it to very widely (Tables 1-6, Figs 1-6).

The secondary callus of rue used as test material in the experiments propagated at a moderate growth intensity under the given conditions, just like in our previous experiments (MARÓTI and DÉKÁNY, 1977). In these experiments the growth rate of the control cultures gave rational values, so it was suitable to determine the effect of the heavy metals (MARÓTI and BOGNÁR, 1988; MARÓTI et al., 1972). The increasing rate of contamination caused by heavy metals makes it necessary to determine the limit of tolerance for the most possible plant speices (DÄSSLER, 1979; KOVÁCS, 1985; KOVÁCS et al., 1986). The metals and their concentrations used were chosen partly on the basis of literary data, partly owing to their frequency as contaminants (FILIPPIS et al., 1981).

The metal ions tested by interfering with various metabolic processes of the plant cells (nucleic acid synthesis, enyzme activity, chloro-

Table 1

Effect of cadmium on the growth of *Ruta* callus tissue

Hormones	$Cd(CH_3COO)_2$		Fresh weight		Dry weight		Number of cells		Daily weight increase		Relative
mg/l	M		g/flask	% of control	%	% of control	10^3 n/g	% of control	mg	% of control	growth
	10^{-4}	$\bar{x}$	0.524	33	1.13	78	6833	133	11.57	24	1.62
		±s	0.037		-0.07		19				
	5.10^{-5}	$\bar{x}$	1.352	87	1.36	94	8445	165	41.14	85	5.76
		±s	0.168		0.12		94				
2,4-D 6	10^{-5}	$\bar{x}$	1.197	77	1.28	89	6014	117	35.60	74	4.98
IAA 4		±s	0.292		0.01		55				
	5.10^{-6}	$\bar{x}$	1.229	49	1.28	89	4419	86	36.75	76	5.14
		±s	0.049		0.08		33				
	10^{-6}	$\bar{x}$	1.273	82	1.42	99	4447	87	38.32	79	5.36
		±s	0.067		0.08		30				
	Control	$\bar{x}$	1.551	100	1.44	100	5125	100	48.25	100	6.75
		±s	0.079		0.14		50				

Table 2

Effect of copper on the growth of *Ruta* callus tissue

Hormones	$CuSO_4$		Fresh weight		Dry weight		Number of cells		Daily weight increase		Relative
mg/l	M		g/flask	% of control	%	% of control	10^3 n/g	% of control	mg	% of control	growth
	10^{-4}	$\bar{x}$	0.161	10	1.51	105	5502	107	-	-	-
		$\pm s$	0.057		0.13		21				
	5.10^{-5}	$\bar{x}$	0.145	9	1.69	117	5969	116	-	-	-
2,4-D 6		$\pm s$	0.024		0.19		24				
	10^{-5}	$\bar{x}$	0.339	22	1.78	124	5387	105	4.96	10	0.69
IAA 4		$\pm s$	0.074		0.14		33				
	5.10^{-6}	$\bar{x}$	0.686	44	1.41	98	6377	124	17.35	36	2.43
		$\pm s$	0.205		0.17		64				
	10^{-6}	$\bar{x}$	0.670	43	1.55	108	4927	96	16.92	35	2.37
		$\pm s$	0.155		0.12		32				
	Control	$\bar{x}$	1.551	100	1.44	100	5125	100	48.25	100	6.75
		$\pm s$	0.079		0.14		50				

Table 3

Effect of mercury on the growth of Ruta callus tissues

Hormones	$HgCl_2$		Fresh weight		Dry weight		Number of cells		Daily weight increase		Relative
mg/l	M		g/flask	% of control	%	% of control	10^3 n/g	% of control	mg	% of control	growth
2,4-D 6 IAA 4	10^{-5}	$\bar{x}$	0.989	64	1.49	103	3387	76	28.17	58	3.97
		$\pm s$	0.185		0.17		27				
	5.10^{-6}	$\bar{x}$	1.400	90	1.44	100	4058	79	42.85	89	6.00
		$\pm s$	0.205		0.17		23				
	10^{-6}	$\bar{x}$	1.415	91	1.53	106	7380	144	43.39	90	6.07
		$\pm s$	0.216		0.12		43				
	5.10^{-7}	$\bar{x}$	1.403	91	1.58	110	7417	145	42.96	89	6.01
		$\pm s$	0.242		0.22		67				
	10^{-7}	$\bar{x}$	1.446	93	1.64	114	7764	151	44.50	92	6.23
		$\pm s$	0.227		0.17		48				
	Control	$\bar{x}$	1.551	100	1.44	100	5125	100	48.25	100	6.75
		$\pm s$	0.079		0.14		50				

Table 4

Effect of nickel on the growth of Ruta callus tissues

Hormones	$NiSO_4$		Fresh weight		Dry weight		Number of cells		Daily weight increase		Relative
mg/l	M		g/flask	% of control	%	% of control	10^3 n/g	% of control	mg	% of control	growth
	10^{-4}	$\bar{x}$	0.185	12	1.63	113	5995	117	-	-	-
		$\pm s$	0.020		0.16		60				
	5.10^{-5}	$\bar{x}$	0.306	20	1.68	117	5150	101	3.87	8	0.53
		$\pm s$	0.030		0.10		28				
2,4-D 6	10^{-5}	$\bar{x}$	0.706	46	1.57	109	5466	107	18.07	37	2.53
IAA 4		$\pm s$	0.140		0.15		94				
	5.10^{-6}	$\bar{x}$	0.994	64	1.53	106	4393	86	28.35	59	3.97
		$\pm s$	0.100		0.10		19				
	10^{-6}	$\bar{x}$	1.478	95	1.48	102	4568	89	45.64	95	6.39
		$\pm s$	0.510		0.50		36				
	Control	$\bar{x}$	0.551	100	1.44	100	5125	100	48.25	100	6.75
		$\pm s$	0.079		0.14		50				

Table 5

Effect of lead on the growth of Ruta callus tissue

Hormones mg/l	$Pb(NO_2)_2$ M		Fresh weight g/flask	Fresh weight % of control	Dry weight %	Dry weight % of control	Number of cells 10^3 n/g	Number of cells % of control	Daily weight increase mg	Daily weight increase % of control	Relative growth
2,4-D 6 IAA 4	10^{-4}	$\bar{x}$	0.784	51	1.41	98	8142	159	20.85	43	2.92
		$\pm s$	0.184		0.10		111				
	5.10^{-5}	$\bar{x}$	0.983	63	1.42	99	5701	111	27.96	58	3.91
		$\pm s$	0.367		0.50		25				
	10^{-5}	$\bar{x}$	1.504	97	1.34	93	5477	107	46.57	97	6.52
		$\pm s$	0.095		0.07		45				
	5.10^{-6}	$\bar{x}$	1.479	95	1.35	94	7016	137	45.67	95	6.39
		$\pm s$	0.248		0.10		183				
	10^{-6}	$\bar{x}$	1.431	92	1.38	96	5247	102	43.96	91	6.15
		$\pm s$	0.486		0.14		45				
	Control	$\bar{x}$	1.551	100	1.44	100	5125	100	48.25	100	6.75
		$\pm s$	0.079		0.14		50				

Table 6

Effect of zinc on the growth of *Ruta* callus tissue

Hormones	ZnSO$_4$		Fresh weight		Dry weight		Number of cells		Daily weight increase		Relative
mg/l	M		g/flask	% of control	%	% of control	10^3 n/g	% of control	mg	% of control	growth
	10^{-4}	$\bar{x}$	0.480	31	1.31	91	4268	83	10.00	21	1.40
		±s	0.171		0.08		27				
	5.10^{-5}	$\bar{x}$	0.719	46	1.16	81	4095	80	18.53	38	2.60
		±s	0.258		0.10		34				
2,4-D 6	10^{-5}	$\bar{x}$	0.806	52	1.12	78	4554	89	21.64	45	3.03
IAA 4		±s	0.146		0.10		39				
	5.10^{-6}	$\bar{x}$	0.824	53	1.22	85	5086	99	22.28	46	3.12
		±s	0.154		0.11		32				
	10^{-6}	$\bar{x}$	0.829	53	1.36	94	6105	119	22.46	47	3.14
		±s	0.175		0.17		64				
	Control	$\bar{x}$	1.551	100	1.44	100	5125	100	48.25	100	6.75
		±s	0.079		0.14		50				

Fig. 1. Effects of various concentrations of cadmium acetate and cadmium ion, respectively, on rue (Ruta graveolens L.) callus tissues, as a percentage to the control
Fresh weight; Dry weight; Number of cells
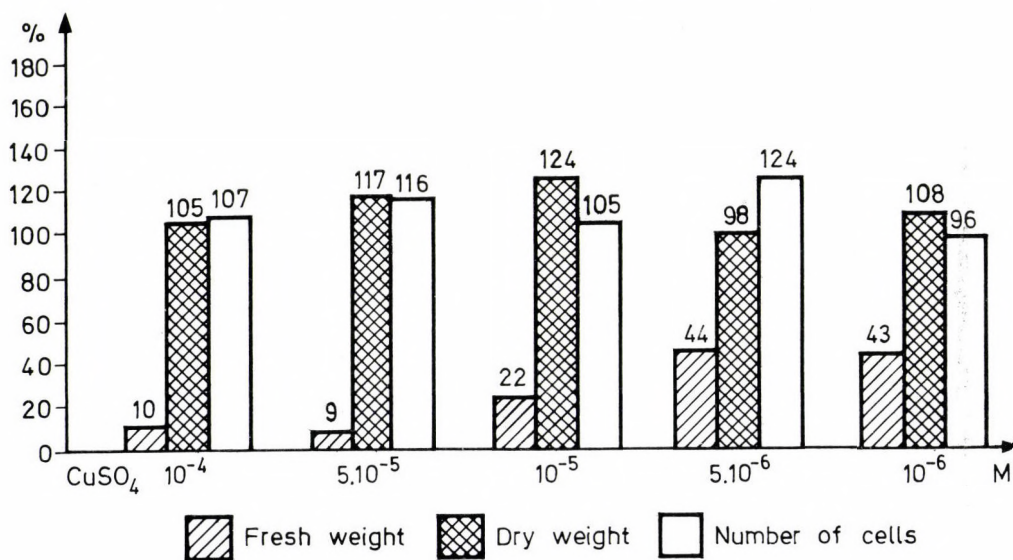
Fig. 2. Effects of various concentrations of copper sulphate and copper metal ion, respectively, on rue (Ruta graveolens L.) callus tissues, as a percentage to the control
Fresh weight; Dry weight; Number of cells
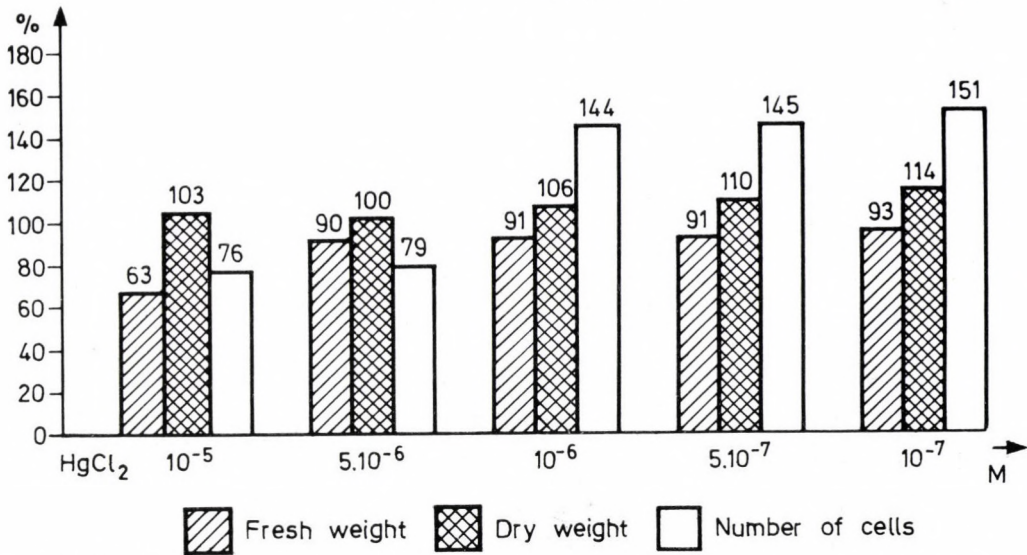
Fig. 3. Effects of various concentrations of mercury chloride and mercury metal ion, respectively, on rue (Ruta graveolens L.) callus tissues, as a percentage to the control ▨ Fresh weight; ▩ Dry weight; □ Number of cells
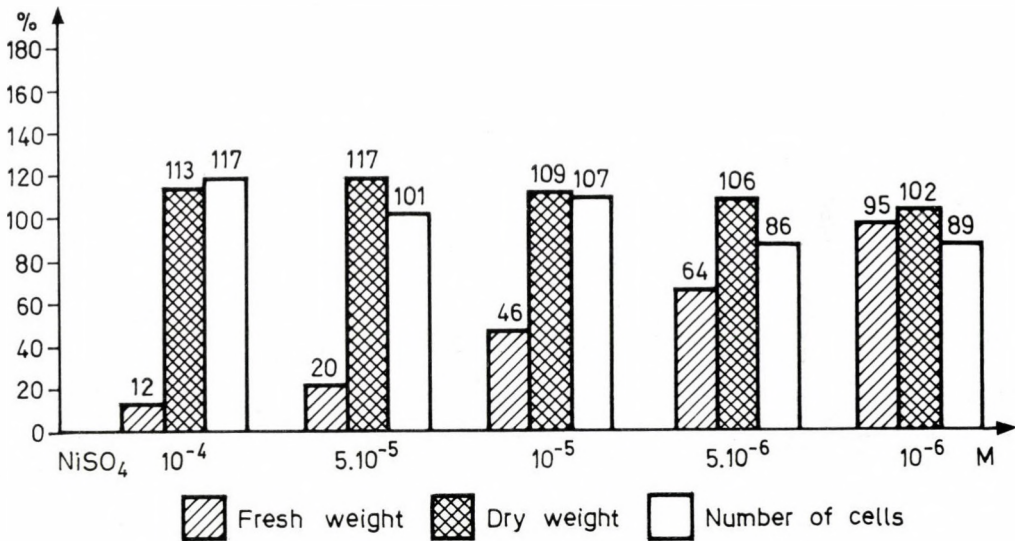
Fig. 4. Effects of various concentrations of nickel sulphate and nickel metal ion, respectively, on rue (Ruta graveolens L.) callus tissues, as a percentage to the control ▨ Fresh weight; ▩ Dry weight; □ Number of cells
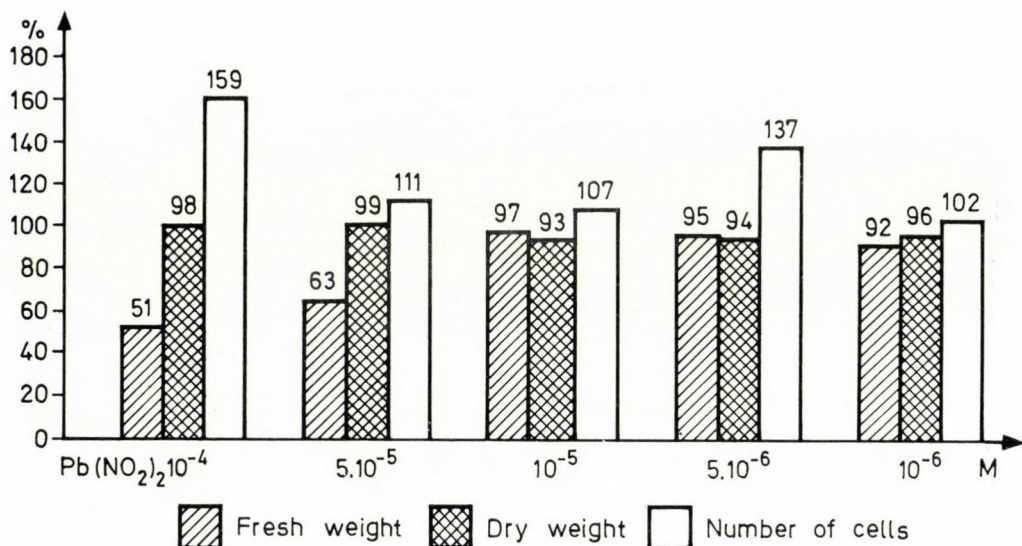
Fig. 5. Effects of various concentrations of lead nitrite and lead metal ion, respectively, on rue (*Ruta graveolens* L.) callus tissues, as a percentage to the control ▨ Fresh weight; ☒ Dry weight; ☐ Number of cells
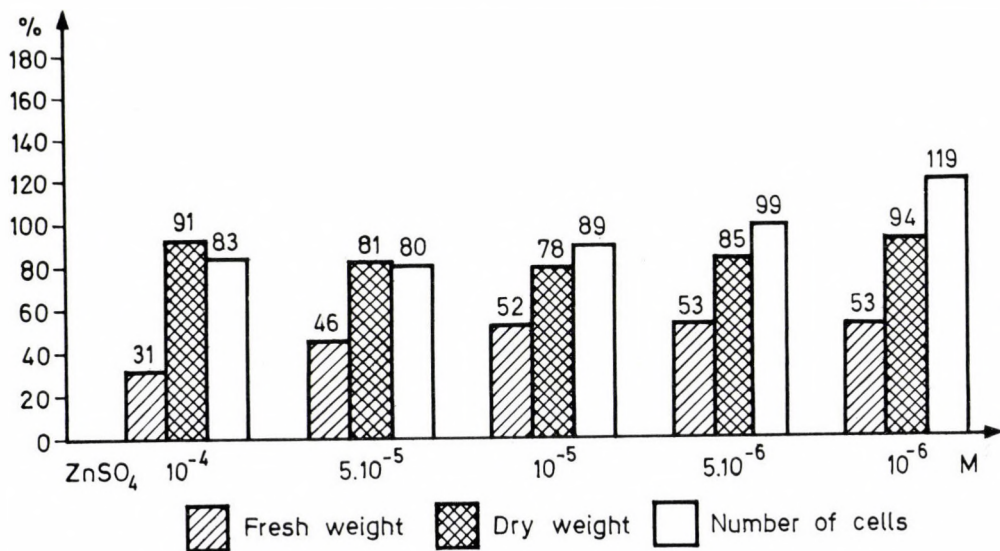
Fig. 6. Effects of various concentrations of zinc sulphate and zinc metal ion, respectively, on rue (*Ruta graveolens* L.) callus tissues, as a percentage to the control ▨ Fresh weight; ☒ Dry weight; ☐ Number of cells

phyll formation, cell division, etc.) cause growth inhibition, and in some cases tissue necrosis as proved by a number of literary data (BONALY et al. 1980; NAG et al., 1981; PAIS, 1980; PATEL et al., 1977; WALLACE, 1977; WALLACE et al., 1977). This influence on the various life processes may then explain, e.g. the opposite tendencies of dry weight and fresh weight shown with the increasing concentrations, or the changes in the number of cells per unit weight, that beside the measured data the converted daily and relative growth indices as well as the figures well characterize (MARÓTI and BOGNÁR, 1985, 1988).

As learnt from the results of the experiments each of the six heavy metals employed inhibits the fresh weight increase of the callus tissue. The inhibition increases with the increase of concentration, but its extent may widely vary with the metal ion applied. The proportion of dry weight is nearly identical with or several per cents higher than that in the control; this is the most stable of the three parameters examined. The number of cells/g callus tissue is the same as in the control, though it may even be larger or smaller - depending on the influence the metal used exercises on the metabolism.

By testing a series of heavy metal concentration on the callus of rue we have obtained useful information on the limit of tolerance of this plant species to the toxic heavy metals examined. Our results suggest that similar tests aimed at establishing the limit of heavy metal tolerance for as many plant species as possible ought to be performed in large numbers if - with a view to our health - the present rate of environment pollution is to be checked.

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Acta Botanica Hungarica 35(1-4), pp. 199-226 (1989)

FLOWER STRUCTURE OF HISTORICAL AND CULTIVATED PLUMS, RELATIONSHIP BETWEEN MORPHOLOGICAL CHARACTERS AND SELF-FERTILITY

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(Received: 8 December 1987)

Morphological studies were carried out over 6 years on flowers of 80 cultivated and historical plum varieties. Neither the 27 characters observed nor the lenght of the investigation period are usual in international studies on the floral biology of fruit species.

The basic morphological characteristics of flower required for telling apart and identifying varieties (median of petal, length of pistil, diameter of stigma, stamen number, relative stamen number, pollen germination, apistillate and polycarpic tendencies of varieties) were established.

The most important morphogenetic characters of flower are in close correlation, so their values are not discretionary. The internal and ecological factors bring about dynamic changes in the flower structure. By the morphological changes the effect of root stock and the consequences of phytotechnical interventions can be verified.

Besides self-fertility some morphological characters of flower also show great dependence on the crop-year. From the point of view of self-fertility the relative stamen number, the stigma diameter, further the apistillic and polycarpic tendency are the most important morphogenetic characters of the flower.

The study convincingly proved the necessary and regular relationship between flower morphology (structure) and self-fertility (function) in plum varieties.

Literary review

The flower structure of the genus Prunus bears many important characters of ancientry, which makes it possible and necessary to settle some phylogenetic (morphological and physiological) questions, on the one hand, and solve a number of cultivation (economic) problems, on the other. According to the results of several years of flower morphology examinations the reliability and informative role of fertility data can be increased. Experiences show that with the species of the subfamily Prunoideae the period of variety evaluation can be shortened, which has a favourable effect in the course of both breeding and acclimatization.

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The Hungarian fruit growers call, in fact, either for turning out new varieties sooner than so far, or for a successful variety and clone selection. However, the diversity of the aspects of examination, the slowness of fertility tests, the high crop-year (climatic) dependence of fertility (actual fertility), the smaller or greater technical difficulties of isolation, the frost damages of flowers, and even more so of fruit primordia render the evaluation of varieties very slow.

In so far as it is true that the variety is a means of production (TOMCSÁNYI, 1980), "it is also the only means of improving the choice that determines the character of the fruit put on the market". The knowledge of fruit variety is an extremely important economic information; the flower is a character of basic importance in identifying and telling apart the varieties.

A reliable and quick examination method for determining and characterizing the fertility in breeding work, variety trials and agrotechnical examinations is equally interesting from theoretical and practical points of view. It is so even when the actual fertility examinations cannot be fully replaced by them, such are e.g. the morphological surveys.

It is not a different case with the research of plum varieties either. Plum is a fruit species of economic importance in Hungary, it represents nearly a quarter of the total stock of fruit trees in the country (HARSÁNYI, 1980). Its share in the commercial orchards of Hungary was earlier relatively restricted, but for about ten years interest in this fruit species has considerably increased. Changes in the consumption demands, the increasing demand for processed plum, the relatively simple technics of cultivation, the wide possibilities of mechanization as well as the fact that plant protection causes no problem may certainly play some role in it. The great choice of variety offers good chances to the growers, that even the question of root-stock would not limit, if only the virus problem did not exist. Both in breeding work and variety research attempts to virus tolerance must be part of the programme even if virus resistance cannot be achieved in the near future.

With varieties of a collection of plum in full bearing we tried to find out whether the flower structure - apart from its being a varietal character - could give or was able at all to give economically useful information. We thought it reasonable to examine the historical varieties because it is of them that the widest and most detailed data of flower and fertility biology are available.

As a consequence of the accelerated change of variety a large proportion of the varieties included in the study - though in process of disappearing - are still suitable for exploring fundamental morphogenetic characteristics and regularities.

In variety research the greatest importance of the numerical examinations of flower morphology consists of the following:

- they are able to disclose the morphological components of fertility,
- whereby the potential self-fertility of varieties, prospective varieties and hybrids becomes easy to assess with a quick method;
- even in early years of flowering and bearing the varieties are easier to identify and tell apart;
- on the basis of the characteristics of flower organs the modifying effects of environment, plant sanitation and phytotechnics can be detected earlier, more rapidly and reliably.

The morphological examination of plum flowers can be traced far back to the past. The characteristics of the andrcecium and gymnoecium (LINNÉ, 1784), the length of petiole (DAHL, 1935; SURÁNYI and TÓTH, 1976), the shape and size of petals (TÓTH, 1957; KÁRPÁTI, 1967), the parameters of stigma and pollen (RÉMY, 1953), the height of stigma related to the anthers (DAHL, 1935; RŐDER, 1940; PLOCK, 1953; KOBEL, 1954; TÓTH, 1957, 1980b), the stamen number (LINNÉ, 1784; HASKELL, 1954; MORRISON, 1964; SURÁNYI and TÓTH, 1977; SURÁNYI, 1979), the size of pistil (WATANABE and YASUNOBU, 1961, SURÁNYI, 1978), the relative stamen number (SURÁNYI, 1973, 1976, 1978, 1980a, 1980b, 1980c, 1980d, 1980e) are all important characteristics of variety and fertility.

Primary and secondary correlation can be discovered in the plum flowers, too, namely between gynoecium and androecium, and between sepals and petals. From the point of view of fertility it is naturally the primary correlation that is of interest, although the size and other characteristics (colour, shape, number) of the petals also influence the conditions of pollination.

The first data suggesting regularity were obtained in 1970 in various stone fruit varieties (SURÁNYI, 1970); the close negative correlation between pistil length and stamen number can be explained by the telome theory. The pistil as a telome member of dominant position, and the telome members of lateral position, i.e. the verticillate stamina show a numerical correlation (cf. SURÁNYI, 1974b).

The "sexual" correlation, that is the relationship between generative organs, proved to be suitable for explaining the fertility conditions (SURÁNYI, 1973), the teratomata (SURÁNYI, 1972), the effects of chemical treatments (SURÁNYI, 1977) and even of root-stocks (SURÁNYI, 1974a, 1985a) and for describing the varieties (SURÁNYI, 1976, 1979, 1980b, 1986a, 1986b).

In the course of our investigations we introduced two new concepts: the relative stamen number expressed by stamen number per unit pistil length, which characterizes the "sexual" conditions; and the ratio of stigma diameter/pollen size which indicates the chances of fertilization (SURÁNYI, 1980a, 1983).

Between 1975 and 1980 the range of the varieties and characteristics examined was substantially widened and the part results were published in detail (SURÁNYI, 1980a, 1980d, 1983). In choosing and characterizing the varieties (disposition to self-fertility, fruit colour) we mostly relied on descriptions by HEDRICK (1911), RÖDER (1940), TÓTH (1957), NICOTRA et al. (1972) and DERMINE and LIARD (1957, 1978), and naturally on our own botanical observations (stamen number, fruit colour).

We wished to give answer to the following questions:

- Which are the most important characters of flower morphology specific of variety?
- How do the flower organs change in size from year to year under given ecological conditions?
- Are the measurement changes of the different morphogenetic characteristics independent or correlated?
- Has self-fertility morphological components in the plum flowers?
- May any relationship exist between the morphological factors of self-fertility and its yearly changes?
- Is it possible to explain changes (in size) or abnormities of flower structure, and disposition to self-fertility (and fertility in general) as a function of the year effects by the correlation of the generative organs?

Material and Method

The flower morphology examinations were carried out between 1975 and 1980 at the Cegléd Station of the Fruit- and Ornamental Growing Research and Development Enterprise. The soil of the variety collection of plum was in good cultural condition favourably supplied with nutrients. The trends of daily temperature and monthly precipitation are shown in Tables 1 and 2. The first half of the investigation period was rainier and warmer than the second half:

Table 1

Trend of the daily average temperature in the examination period

(data from the Meteorological Station of Cegléd)

Month	1974	1975	1976	1977	1978	1979	1980	Average °C	Average of 25 years
January		2.2	1.0	- 0.2	- 0.7	- 2.8	- 4.3	- 1.6±2.4	- 1.8
February		0.9	- 1.9	4.4	- 0.2	1.9	1.5	1.1±2.1	0.7
March		9.0	2.3	8.4	6.8	8.5	4.7	6.6±2.6	5.4
April		10.3	11.6	9.4	9.9	9.8	8.8	10.0±9.5	11.4
May		18.0	16.2	16.4	13.9	16.4	13.1	15.7±1.8	16.7
June	18.7	19.6	19.4	19.8	18.3	21.9		19.6±1.2	20.2
July	21.6	20.3	22.3	20.2	18.8	19.4		20.4±1.3	21.7
August	23.4	20.5	18.8	19.5	18.5	19.8		20.1±1.8	20.7
September	17.2	17.5	15.1	13.8	15.5	17.5		16.1±1.5	16.5
October	8.0	11.1	11.8	11.2	11.6	9.4		10.5±1.5	11.0
November	5.9	3.4	6.5	5.3	2.1	5.8		4.8±1.7	5.6
December	3.1	0.6	0.7	- 2.3	0.7	4.1		1.1±2.2	0.8
Average		11.1	10.3	10.4	9.6	10.9			10.7

Table 2

Trend of monthly precipitation in the examination period

(data from the Meteorological Station of Cegléd)

Month	1974	1975	1976	1977	1978	1979	1980	Average ^{o}C	Average of 30 years,mm
January		10.0	38.4	41.5	11.8	60.1	33.2	32.5±19.0	29.6
February		5.8	2.4	76.9	22.8	26.7	13.5	24.7±27.2	28.9
March		33.4	52.5	47.2	23.3	26.5	31.5	35.7±11.6	25.8
April		59.5	68.2	22.3	43.5	46.7	44.8	47.5±15.7	41.9
May		82.6	10.4	19.2	101.8	21.0	40.7	45.9±37.7	48.1
June	67.2	77.3	36.4	29.7	83.9	43.4		56.3±22.8	73.9
July	55.4	115.5	49.5	39.4	55.2	69.5		64.1±27.0	53.6
August	71.9	104.6	35.9	14.7	27.4	69.9		54.1±33.8	46.7
September	32.9	62.5	83.3	32.4	17.1	3.8		38.7±29.4	33.8
October	159.4	34.4	51.2	8.6	8.2	21.7		47.3±57.3	36.1
November	71.5	26.7	36.9	63.3	9.3	61.2		44.8±24.4	53.8
December	23.5	46.8	85.6	21.1	41.5	44.8		43.9±23.2	44.5
Total		659.1	550.7	416.3	445.8	495.2			516.7

Crop-year	Average temperature, ^{o}C	Total precipitation, mm
1974/75	11.5	673.1
1975/76	10.2	639.9
1976/77	11.1	585.9
1977/78	9.8	412.4
1978/79	9.9	423.6
1979/80	10.1	478.0

The trees were planted in 1954/55 at a spacing of 8x7 m, with 5-fold replication. The obviously virus infected trees were excluded from the study on the basis of repeated surveys. After appropriate preliminary examinations spurs with buds and opening flowers were collected from branchlets of the southern arms of 3 trees of each variety.

From each variety 30 flowers were processed. Weight, length of petiole, diameter of stigma and number of fertile and sterile stamina were recorded for each flower (number of replications: 30). For every three flowers the length of the calyx tube, the lengths and widths of the sepals and petals as well as the length of filaments in the outer and inner circle of stamina were measured (replications: 10).

Further, in every nine flowers the length and width of anther and pollen were also measured for each of the 80 varieties (replications: 4). The tube-developing capacity of pollen was studied in laboratory, in 10% saccharose, by incubation at 21 ^{o}C.

The flowers were weighed by assay balance (cg), the size of the flower parts was determined with millimetre accuracy. The stigma diameter and the size of the anther were established under a binocular microscope at 25x magnification. The pollen measurements and the value of tube development were obtained at a 640x magnification under light microscope, by means of an objective-micrometer again.

Teratomata affecting the gynoecium and androecium were determined in percentage for 30 flowers per year and variety. The absence of pistil is called apistilly, the multiplication of pistil polycarpy, and the petal-like formation of the anther or stamen is the phenomenon of staminody.

The calculated values were obtained from the respective basic data:
- relative stamen number (number of fertile stamina/pistil length),
- sepal-, petal-, anther- and pollen shape index (length/width),
- petal median (average of length and width),
- stigma diameter/pollen size (only the 1st, 10th, 19th and 28th flower were taken into account for stigma diameter),
- the frequency of apistillate, polycarpous and staminodous flowers which play a direct role in flower fertilization was calculated in percentage.

Of the 27 characters the following were included in the study:
- flower weight, cg (n = 30),
- petiole length, mm (n = 30),
- petal median, mm (n = 10),
- pistil length, mm (n = 30),
- stigma diameter, um (n = 30),
- stamen number (n = 30),
- relative stamen number, n/mm (n = 30),
- length of stamen in the outer circle, mm (n = 10)
- pollen size, um (n = 4),
- pollen germination, % (n = 4),
- ratio of stigma diameter/pollen size (n = 4),
- apistilly, %
- polycarpy, %
- staminody, % .

The results of examination were mathematically evaluated (SVÁB, 1981), and so were the meterological data.

To compare the varieties and crop-years series of variance analyses were performed. Differences between the varieties were analysed every year, but the paper only contains the main averages of the six years, and the values of scatter.

Calculations for a total of 325 correlations of the major features were made, but only the correlations of the most important 14 characters were pointed out on the basis of 78 regression analyses (SURÁNYI, 1985b), and some pairs of relationship were included in the study. The relation of the different characteristics ot staminody was left out of the evaluation, since the fact and extent of phyllody is in close correlation only with the size of pistil and number of stamina, and this is expressed by the data of Table 7 calculated from the correlations of the generative organs. Graphic representations are thus shown in the paper for four highly characteristic correlations.

We chose several plum varieties examined for self-fertility (TÓTH et al.) between 1975 and 1980 at Cegléd to compare self-fertility and outstandingly important morphogenetic features by setting series of data side by side. Another important question to be settled was the connection of the relative heights of stigma and anthers with the varieties' disposition to self-fertility.

The examinations covered 26 self-fertile, 13 partially self-fertile, 11 practically self-sterile and 30 self-sterile varieties. The varieties were distributed by colour as follows: 32 were blue-, 26 lilac-, 5 red-, 12 yellow- and 5 green-skinned; and by stamen number: 7 varieties had 20 stamina, 24 of them 25 stamina, 38 had 30 and 11 varieties 35 stamina each. Classification by the last two characteristics was based on our own investigations, while in grouping by the extent of self-fertility we mostly relied on literary data (Table 3).

Detailed examinations of 30 flowers from each of 80 varieties meant, in fact, working up 14000 flowers in six years.

Table 3

Characterization of the varieties examined on the basis of literary data and our own observations

Variety	Stamen number	Fertility conditions	Fruit colour
1. Ageni 1	30	self-fertile	lilac
2. Ageni 2	30	partially self-fertile	lilac
3. Althann	30	practically self-sterile	lilac
3. Alutscha	30	self-sterile	lilac
5. Angouleme greengage	30	self-fertile[2]	green
6. Bavay	25	self-fertile[3]	yellow
7. Beregi datolya	20	self-fertile[9]	blue
8. Beregi vörös	25	self-fertile[x]	lilac
9. Besztercei muskotály	20	self-fertile	blue
10. Besztercei szilva	20	self-fertile	blue
11. Bosznia királynője	25	self-fertile	blue
12. Brassai	30	self-sterile	lilac
13. Burdett Angelina	30	self-sterile	blue
14. Burton	35	self-sterile[4]	lilac
15. Bühli korai	25	self-fertile	blue
16. Coates	35	self-fertile[4]	lilac
17. Cár szilva	30	self-fertile	blue
18. Charcuty	35	self-sterile[5]	red
19. Columbia	25	self-sterile	red
20. Csúcsos szilva	25	practically self-sterile	green
21. Dániel	25	self-sterile	blue
22. Dewett	30	self-sterile	lilac
23. Egger Gusztáv	30	self-fertile	yellow
24. Englebert herceg	25	partially self-fertile	blue
25. Francia narancsszilva	30	self-fertile	yellow

Table 3 (cont.)

Variety	Stamen number	Fertility conditions	Fruit colour
26. Frankfurti szilva	30	self-sterile[3]	blue
27. Golden sugar	35	self-sterile[6]	yellow
28. Gömöri nyakas	30	partially self-fertile	blue
29. Haffner őszi	25	partially self-fertile	lilac
30. Harris monarch	35	self-fertile[7]	red
31. Herrnhausi	30	practically self-sterile[10]	lilac
32. Honey moon	25	self-sterile[8]	yellow
33. Imperial	25	self-sterile	blue
34. Jodoigne	30	self-sterile	lilac
35. Katalán szilva	20	self-sterile	blue
36. Kék tojás	25	partially self-fertile	blue
37. Kék uri	25	self-fertile	blue
38. Késői muskotály	35	self-sterile	blue
39. Kirke szilva	30	self-sterile	blue
40. Korai kedvenc	30	partially self-fertile	blue
41. Leppermann Emma	25	self-fertile[2]	lilac
42. Letricourt	25	self-fertile	yellow
43. Lőwei szép	30	partially self-fertile	blue
44. Mammut Dorota	25	partially self-fertile[11]	lilac
45. Milánói császár	35	self-fertile	blue
46. Mirabellák királynője	30	self-sterile	blue
47. Montfort	30	self-sterile	blue
48. Nagybányai Besztercei	20	self-fertile	blue
49. Nagy cukor	25	partially self-fertile	blue
50. Nagyherceg	30	practically self-sterile	blue
51. Nancy ringló	30	self-sterile	lilac
52. Olasz kék	30	self-fertile	blue
53. Ontario	30	self-fertile	yellow
54. Pacific	20	self-sterile	lilac
55. Piros tojás	30	partially self-fertile	red
56. Pond magonca	35	self-sterile	lilac
57. Primate	35	practically self-sterile	lilac
58. Procureur	30	partially self-fertile	lilac
59. Prugna d'Italia	25	self-fertile[12]	lilac
60. Ruth Gerstetter	25	practically self-sterile	blue
61. Sárga kajsziszilva	30	self-sterile	yellow
62. Sárga uri	30	self-sterile	yellow
63. Sasbachi korai	20	practically self-sterile	blue
64. Sötétkék tojás	30	practically self-sterile	blue
65. Szent Katalin	30	practically self-sterile	yellow
66. Szigeti zöld	25	self-sterile	green
67. Tarka perdrigon	30	self-fertile	lilac
68. Tragédia	30	self-sterile	blue
69. Toursi nagy	25	self-sterile[13]	lilac
70. Lhinksz ringlója	35	self-sterile[14]	lilac
71. Vinke korai	35	self-sterile[15]	green
72. Violaszínű perdrigon	30	practically self-sterile	lilac
73. Violaszínű ringló	25	partially self-fertile	lilac
74. Vörös nektarin	25	self-sterile	lilac
75. Vörös szilva	30	self-fertile	lilac

Table 3 (cont.)

Variety	Stamen number	Fertility conditions	Fruit colour
76. Walesi herceg	30	self-fertile	red
77. Wangenheimi	30	self-fertile	blue
78. Waschmann Berta	30	partially self-fertile	blue
79. Washungton	25	self-sterile	yellow
80. Zöld ringló (greengage)	30	practically self-sterile	green

TÓTH (1957 and 1980a) - unmarked
2) TÓTH (1967)
3) JOHANSSON (1967)
4) GOURIEY - HOWLETT (1941)
5) BERNHARD et al. (1951)
6) BROOKS - OLMO (1960)
7) CRANE (1925)
8) BROOKS - OLMO (1952)
9) SURÁNYI (1973-75 average): 16.2%
10) SURÁNYI (1973-75 average): 0.2 %
11) SURÁNYI (1975-77) average): 4.8 %
12) SURÁNYI (1975-77 average): 14.5 %
13-15) SURÁNYI (1973-75 average): 0.0 %

x Vörös szilva local variety

self-fertile	- 10.0 %
partially self-fertile	2.0 - 9.9 %
practically self-sterile	0.1 - 1.9 %
self-sterile	0.0

Results and Discussion

While plum varieties considerably differ in the mass of flower, differences between them in the length of petiole are much smaller. Thus, the length of petiole shows wider yearly fluctuations than the mass of flower.

Pistil size, stamen number, relative stamen number and stigma diameter are features characteristic of the variety; out of them it is first of all the length of petiole that changes in function of the crop-year. The relative stamen number is rather stable, though it is responsive to the ecological factors; it is, otherwise, related with self-fertility.

The length of filaments in the outer circle is much more a function of the crop-year than of the variety, consequently the relative heights of stigma and anthers may even vary from year to year in the same variety.

Table 4

Comparison of variety- and crop-year effects, and average scatter of the morphological features of flower

Parameters	Variety		Crop-year	
	F-value	Average	F-value	Average
Flower weight, cg	25.42	9.2+0.2	0.44	9.3+0.1
Petal length, mm	1.48	11.3+0.3	1.51	11.2+0.2
Petal median, mm	32.17	10.1+0.6	0.58	10.1+0.3
Pistil length, mm	442.96	12.1+0.3	0.53	12.1+0.1
Stigma diameter, µm	620.70	1009+ 45	1.26	1008+12
Stamen number, n	76.31	26.3+0.8	0.98	26.1+04
Relative stamen number, n/mm	15.33	2.20+0.13	0.29	2.20+0.04
Filament length, mm	769-85	8.1+0.5	1.38	8.2+0.3
Pollen size, µm	196.28	49.5+2.8	1.69	49.0+0.7
Pollen germination, %	659.93	50.6+7.0	2.84	50.7+2.2
Stigma diameter/pollen size	899.56	22.2+2.4	1.15	22.0+0.3
Apistilly, %	46.40	3.6+3.8	1.62	1.5+0.7
Polycarpy, %	49.22	0.9+1.5	3.25	3.4+2.8
Staminody, %	20.91	8.2+6.3	10.20	8.5+2.0
F value 5%	1.32		2.23	
F value 1%	1.47		3.06	
F value 0.1%	1.68		4.10	

The size of pollen fluctuates within very narrow limits depending on the variety; nevertheless, pollen germination suggested a considerable year effect. Substantial differences were not naturally shown by the varieties either in pollen size or in the percentage of tube development.

Abnormities affecting fertility, such as apistilly, polycarpy, staminody, are also phenomena characteristic of the variety but they are influenced by the crop-year as well (Table 4).

Thus, according to Table 4 only pollen germination, polycarpy and staminody show considerable responsiveness to crop-year and climatic factors. Out of the 14 characteristics the ones proved specific of variety and suitable for use in selection and acclimatization work are:

- petal median, mm
- pistil length, mm
- stigma diameter, µm
- stamen number, n
- relative stamen number, n/mm
- pollen germination, % µm

Table 5

Yearly fluctuation of flower morphology data

Characteristics	Years						F-value	$SD_{5\%}$
	1975	1976	1977	1978	1979	1980		
Petal median, mm	10.1	9.9	10.2	10.0	10.2	10.0	0.58	0.27
Pistil length, mm	12.1	12.2	11.9	12.2	12.2	12.1	0.53	0.19
Stigma diameter, μm	1012	1010	1027	1007	1000	993	1.26	34.80
Stamen number, n	25.7	25.8	26.1	26.1	26.2	26.8	0.98	0.57
Relative stamen number, n/mm	2.17	2.17	2.28	2.21	2.18	2.20	0.29	0.09
Pollen germination, %	49.9	51.8	50.9	46.9	53.2	51.6	2.84	3.06
Apistilly, %	0.6	1.2	1.7	1.1	2.6	1.6	1.62	1.26
Polycarpy, %	1.9	1.9	1.5	7.5	6.5	1.3	3.25	2.16
Staminody, %	6.9	10.6	6.3	10.8	9.4	7.1	10.20	3.24

Table 6

Correlations of major morphogenetic characters in plum varieties

Correlations			r-value
Petiole length	-	Pistil length	+ 0.2496^{x}
Petal median	-	Relative stamen number	- 0.7200^{xxx}
Petal median	-	Length of filaments in the outer circle	+ 0.8421^{xxx}
Pistil length	-	Stamen number	- 0.7094^{xxx}
Stigma diameter	-	Pollen size	+ 0.5652^{xxx}

^{x}p = 5%; ^{xxx}p = 0.1%

Table 7

Effect of disorders of reproductive organs on the normal "sexual" region

Parameters	Type of flower		
n = 533	Polycarpous	Normal	$SD_{5\%}$
Pistil length, mm	11.8	12.1^{x}	0.24
Stamen number, n	28.1	27.8	0.12
Relative stamen number, n/mm	2.38	2.30	0.09
n = 195	Deficient	Normal	
Pistil length, mm	0.0	12.4^{xxx}	-
Stamen number, n	29.4^{xxx}	25.9	0.77
Relative stamen number, n/mm	0.0	2.09^{xxx}	-
n = 1265	Staminodous	Normal	
Pistil length, mm	12.5^{x}	12.2	0.14
Stamen number, n	24.2	26.1^{xx}	0.64
Relative stamen number, n/mm	1.94	2.14$^{\oplus}$	0.18

$^{\oplus}$p = 10%; ^{x}p = 5%; ^{xx}p = 1%; ^{xxx}p = 0.1%
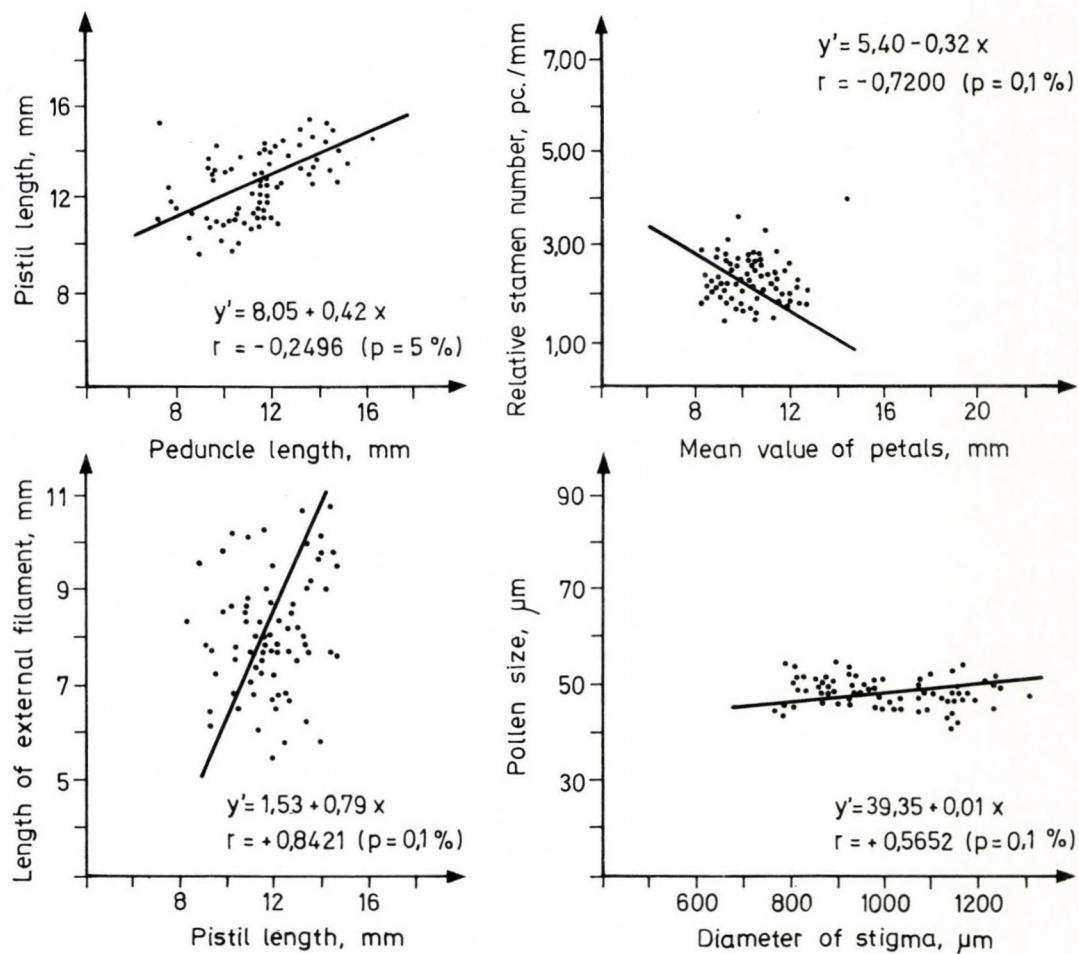
Fig. 1. Important relationships between floral parts of plums
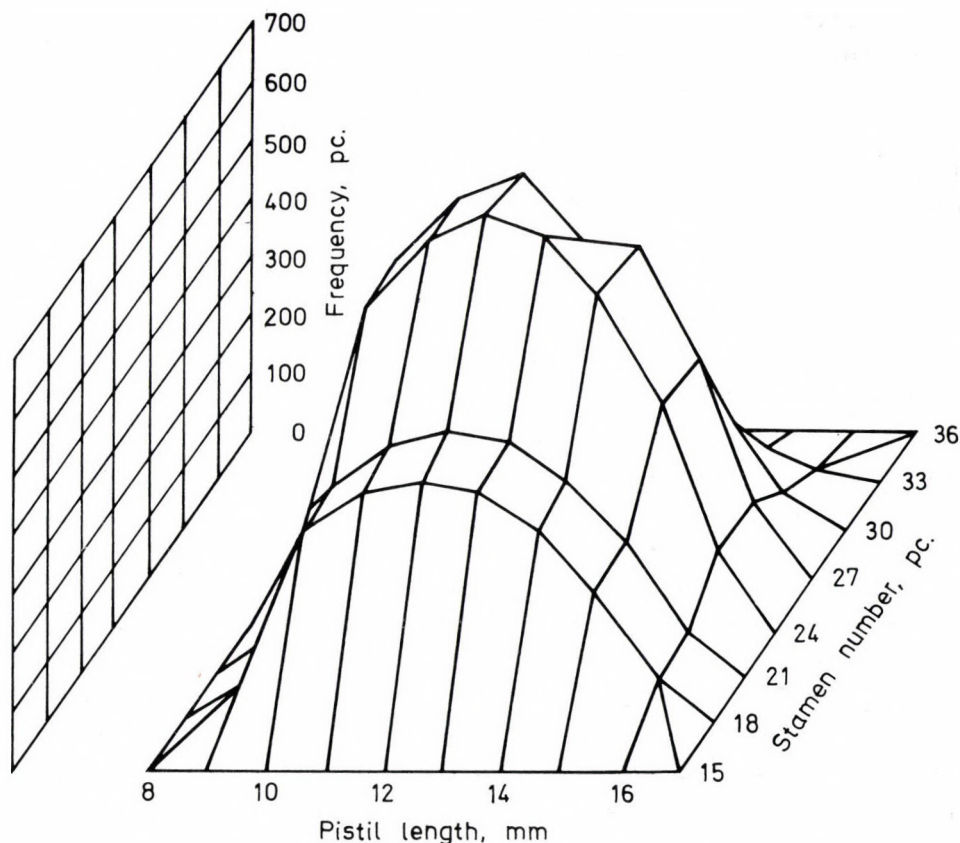
Fig. 2. Correlations between pistil length and stamen numbers of plums

- apistillic and
- polycarpic disposition of variety, %.

The year effects are contained in Table 5. The data only cover 9 characteristics; the less important data can be found in a comprehensive work of ours (cf. SURÁNYI, 1985b).

Changes in the measurements of the most important flower parts, and the correlations thereof called attention to many regular relationships.

The correlative conditions of the components of flower suggest that they are closely connected with one another and change dynamically. Out of the results presented in the paper those concerning the length of petiole and size of pistil, the petal median and relative stamen number, the stigma diameter and pollen size, the size of pistil and length of filaments in the

outer circle, further the highly important "sexual" correlation between pistil length and stamen number should be underlined (Table 6).

According to the results of variety- and crop-year examinations the dynamical morphological changes of flower sometimes may be unfavourable (deficient flower without pistil, many deficient pistils or even a single undeveloped pistil in the flower), while in other cases they are favourable (better developed pistil, larger stigma diameter, higher percentage of pollen tube development). The disorders of gynoecium organization can also be explained by the correlations between the generative organs. In flowers without pistils there are much more stamine than in normal flowers of the same plum variety (Table 7 and Fig. 1).

The data of pistil length and stamen number are of normal distribution, so the main correlation between the two generative organs is really decisive (Fig. 2).

There are mathematical differences in the correlation between generative organs as a function of the varieties' disposition to self-pollination. The androecium is much more responsive to changes in pistil length in the self-fertile and partially self-fertile varieties than in the self-sterile ones, as indicated by the change, or disposition to change of the number of stamina (Table 8, Fig. 3). The major points of the straights calculated from the two variety groups formed the basis of model calculation, the two series of numbers significantly differed in relative stamen number (Table 8).

Stamen numbers, fertility conditions and fruit colours for the 80 plum varieties examined are given in Table 3. The petal median, pistil length and pollen germination follow a decreasing trend with the numerical increase of stigma diameter and androecium, the stamen number and the relative number of stamina obviously increase in each group. In plum varieties with 30-35 stamina the disorders of gynoecium are more frequent than in groups with a lower number of stamina. On the other hand, partial or complete phyllody (staminodes, antherophyllic flowers) most likely occurs in flowers with 20 stamina (Table 9).

The relative stamen number is lowest in the partially self-fertile varieties, in the self-sterile ones it is generally very high, while the self-fertile plum varieties are characterized by intermediate values.

In consequence of ecological effects or under the influence of the root-stock the disposition for self-pollination in the partially self-fertile (large-petalled) plum varieties - which are considered feminine - may
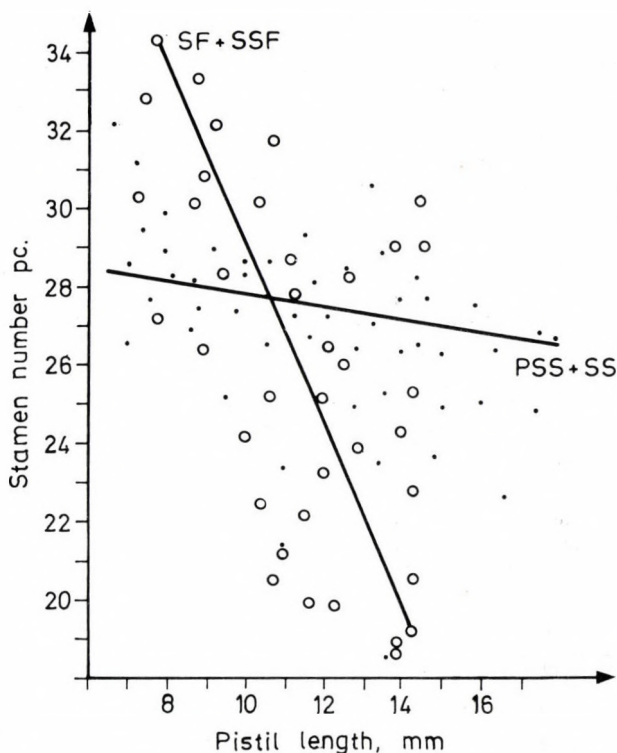
Fig. 3. Correlations between pistil length and stamen number in the plowers of self-fertile + semi-self-fertile and the self-sterile + practically self-sterile plums

improve just as it improves in the masculine varieties (with small petals and a high relative stamen number), only in an opposite way: weakening of the gynoecium of feminine varieties and strengthening of the androecium of masculine varieties are equally favourable from the point of view of self-fertility (Table 10).

Interesting differences can be observed between the groups on the basis of fruit colour as well, namely, the non-blue and non-lilac colour as a recessive character (cf. TÓTH and SURÁNYI, 1980) is closely connected with the flower organs, or in other words: recessivity has an influence on them. First of all the red-skinned varieties should be mentioned in this context, and it is not negligible either that from blue to green the number of stamina steadily rises, but even a decrease in the length of the pistil does not break the increasing trend of the relative stamen number.

The partially self-fertile varieties, that is the ones with a long pistil and few stamina, furthermore the yellow-, red- and green skinned

Table 8

Values of relative stamen number calculated from points corrected on the basis of "sexual" regression curves

Pistil length mm	Self-fertile and partially self-fertile varieties		Practically self-sterile and self-sterile varieties	
	Relative stamen number n	Frequency %	Relative stamen umber n	Frequency %
8	4.16	1.4	3.50	2.5
9	3.45	3.5	3.10	6.3
10	2.88	4.4	2.78	5.5
11	2.43	9.3	2.51	7.5
12	2.03	40.1	2.28	14.3
13	1.71	21.8	2.09	24.8
14	1.41	10.4	1.93	32.6
15	1.16	4.0	1.79	4.3
16	0.94	5.1	1.67	2.2
Weighted average	2.177		2.457^{xx}	
Direct average	2.241		$2.407^{⊕}$	

$^{⊕}p = 10\%$; $^{xx}p = 1\%$

Table 9

Changes in the specific characters of variety groups set up by stamen number

Specific characters	Stamen number 20	25	30	35	$SD_{5\%}$
Petal median, mm	10.0	10.3	10.1	9.8	0.14
Pistil length, mm	13.3	12.8	12.0	11.2	0.33
Stigma diameter, µm	1002	1062	1000	937	48.9
Stamen number, n	19.1	23.6	27.8	31.7	0.62
Relative stamen number, n/mm	1.52	1.93	2.35	2.83	0.16
Pollen germination, %	56.5	52.4	50.2	41.2	3.31
Apistilly, %	2.7	2.2	4.0	4.5	1.75
Polycarpy, %	0.1	0.9	1.6	2.8	2.60
Staminody, %	26.9	9.8	4.9	7.1	8.43

Table 10

Changes in the variety specific characters of fertility groups

Specific characters	Fertility groups				$SD_{5\%}$
	SF	PSF	PSS	SS	
Petal median, mm	10.3	11.7	10.0	10.9	0.36
Pistil length, mm	12.3	12.9	12.4	11.6	0.21
Stigma diameter, μm	1038	985	1005	967	38.69
Stamen number, n	25.0	25.7	25.9	27.7	0.29
Relative stamen number, n/mm	2.05	1.90	2.12	2.42	0.04
Pollen germination, %	61.4	52.1	47.8	44.3	4.12
Apistilly, %	2.5	6.9	3.4	2.0	2.29
Polycarpy, %	1.1	1.5	0.8	2.0	2.06
Staminody, %	13.8	12.5	3.9	4.9	4.14

Abbreviations: SF = self-fertile (above 10.0%)
PSF = partially self-fertile (2.0 - 9.9%)
PSS = practically self-sterile (0.1 - 1.9%)
SS = self-sterile (below 0.1%)
(TÓTH, 1967)

Table 11

Changes in the variety specific characters of fruit colour groups

Specific characters	Fruit colour					$SD_{5\%}$
	blue	lilac	red	yellow	green	
Petal median, mm	10.6	10.0	9.5	10.4	9.4	0.18
Pistil length, mm	13.5	12.9	12.8	12.5	11.9	0.21
Stigma diameter, μm	985	1035	1135	978	966	22.03
Stamen number, n	25.1	26.5	27.9	27.5	28.6	0.35
Relative stamen number, n/mm	2.07	2.27	2.26	2.25	2.49	0.49
Pollen germination, %	51.5	52.2	49.8	45.4	49.8	1.96
Apistilly, %	2.6	4.1	5.9	3.5	3.3	2.61
Polycarpy, %	2.2	1.1	2.0	0.8	0.3	1.63
Staminody, %	10.8	8.4	7.0	1.0	8.7	2.24
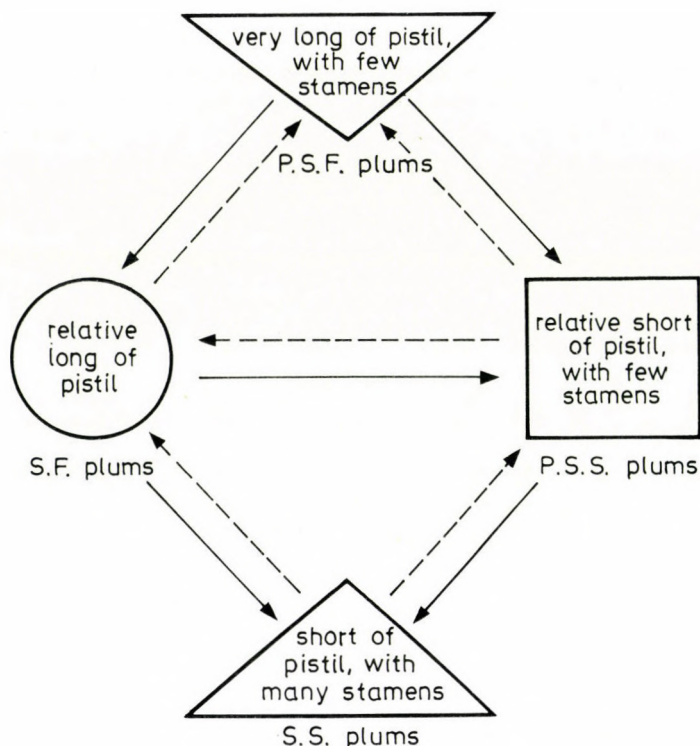
Fig. 4. A scheme of sex reversions in plum varieties; ⟶ = masculinization, ---> = feminization

plums are particularly inclined to form teratomata of reproductive organs (Table 11).

The chance of self-pollination generally decreases in varieties with a lower than 1.30/mm (partially self-fertile) and higher than 1.70/mm (self-sterile varieties) relative stamen number, because in those cases the flower is either too feminine or too masculine, and the other reproductive organ is in a disadvantageous position. The size of flower together with the length of pistil and number of stamina is suitable to illustrate the above, moreover, the ratios also indicate the size of the flowers well. The other part of Fig. 4 shows the favourable or unfavourable nature of "sexual" changes characterized by the relative stamen number (Fig. 4).

The basic morphogenetic characteristic shown in Table 8 clearly reflects the yearly changes, just as the results of pollination tests do (Table 12), even if they were not carried out by us in the past period. Table 12 testifies the importance of self-pollination and the role of the pollinator partners; the different successfulness of pollen donors as a func-

Table 12

Crop-year dependence of self- and free-pollination in some plum varieties

(on the basis of literary data)

Variety		Years				
		Crop-year dependence of self-pollination				
		1950	1951		average	CV, %
Besztercei szilva		12.5	22.3		17.4 ± 6.9	39.8
Althann		0	0		0	-
Ageni		24.7	40.7		32.7 ±11.3	5.7
Zöld ringló (Greengage)		0.2	0.1		0.15± 0.07	47.1
Olasz kék		10.3	4.9		7.6 ± 3.8	50.2
(TÓTH, 1957)						
		1969	1970		average	CV, %
Althann		0	0		0	-
Casalinga		12.3	12.3		12.3 ± 0.0	0.0
Pożegača		8.6	19.0		13.8 ± 7.3	53.3
Stanley		13.5	5.6		9.6 ± 5.6	58.2
(FACCIOLI - REGAZZI, 1972)						
		Crop-year dependence of free-pollination				
♀	♂	1963	1963	1965	average	CV, %
Althann	Besztercei szilva	12.5	11.4	10.4	11.4 ± 1.05	9.2
	Ageni 2	16.8	9.8	16.1	14.2 ± 3.86	27.1
Debreceni muskotály	Ageni 2	19.5	12.7	11.9	14.7 ± 4.18	28.2
	Althann	12.3	9.6	3.8	8.6 ± 4.34	50.5
	Olasz kék	13.7	12.5	11.3	12.5 ± 1.20	9.6
	Zöld ringló	8.2	3.9	11.2	7.8 ± 3.67	47.0
Zöld ringló	Ageni 2	3.6	10.8	19.0	11.1 ± 7.71	69.4
	Besztercei szilva	3.6	5.9	15.6	8.4 ± 6.37	75.8
	Besztercei muskotály	3.5	3.7	11.3	6.2 ± 4.45	71.7
(TÓTH, 1980)						

Table 13

Low and high position stigma as a disputed character of self-fertility in the plum varieties examined

Fertility groups	Stigma below (low) the anthers	Stigma above (high) the anthers
Self-fertile and partially self-fertile	31 (29.6%)	6 (7.4%)
Practically self-sterile and self-sterile	33 (34.4%)	10 (8.6%)

$Chi^2 = 0.645$

Table 14

Comparison of plum varieties for morphological features of flower influencing self-fertility

Variety	Relative stamen number n/mm	Stigma diameter μm	Apistilly %	Polycarpy %
1. Ageni 1	2.27 ± 0.24	1001 ± 36	1.1 ± 0.0	0
2. Ageni 2	2.59 ± 0.09	897 ± 43	18.5 ±25.0	0
3. Althann	2.78 ± 0.23	1322 ± 67	1.7 ± 0.0	1.7 ± 0.0
4. Alutscha	3.22 ± 0.31	819 ± 49	6.1 ± 7.4	0.6 ± 0.0
5. Angouleme-i ringló	1.84 ± 0.09	1169 ± 43	9.4 ±14.0	1.1 ± 0.0
6. Bavay	1.76 ± 0.06	1022 ± 49	0	0.6 ± 0.0
7. Beregi datolya	1.32 ± 0.06	788 ± 46	8.7 + 0.0	0
8. Beregi vörös	2.26 ± 0.09	888 ± 32	0	1.1 ± 0.0
9. Besztercei muskotály	1.38 ± 0.13	1152 ± 36	7.2 ± 8.0	0
10. Besztercei szilva	1.37 ± 0.15	1153 ± 60	0	0.6 ± 0.0
11. Bosznia királynője	1.84 ± 0.16	1096 ± 58	0	0
12. Brassai	2.13 ± 0.12	1030 ± 41	0	0
13. Burdett Angelina	2.83 ± 0.12	884 ± 53	13.9 ± 2.6	1.4 ±19.9
14. Burton	2.85 ± 0.27	798 ± 35	1.9 ± 4.0	0
15. Bühli korai	1.72 ± 0.02	879 ± 44	5.1 ± 7.9	0
16. Cár szilva	2.56 ± 0.14	990 ± 65	0	0
17. Charcuty	2.52 ± 0.26	1156 ± 48	0	0
18. Coates	2.76 ± 0.09	811 ± 15	0.3 ± 0.0	0
19. Columbia	2.22 ± 0.16	1136 ± 42	0	3.3 ± 4.2
20. Csúcsos szilva	2.00 ± 0.15	925 ± 46	18.9 ±32.4	0.6 ± 0.0
21. Dániel	2.25 ± 0.13	940 ± 49	0	0
22. Dewett	2.53 ± 0.13	777 ± 11	5.8 ± 7.6	0
23. Egger Gusztáv	2.13 ± 0.09	906 ± 26	0	0
24. Englebert herceg	1.61 ± 0.13	904 ± 30	1.7 ± 0.0	0
25. Francia narancsszilva	1.93 ± 0.05	1102 ± 30	2.2 ± 4.0	0

Table 14 (cont.)

Variety	Relative stamen number n/mm	Stigma diameter μm	Apistilly %	Polycarpy %
26. Frankfurti szilva	2.61 ± 0.14	933 ± 31	0	0.6 ± 0.0
27. Golden sugar	2.68 ± 0.13	877 ± 62	0.8 ± 1.4	0
28. Gömöri nyakas	2.16 ± 0.11	837 ± 27	0	0
29. Haffner őszi	1.65 ± 0.12	909 ± 24	0	0
30. Harris Monarch	2.10 ± 0.22	925 ± 37	3.3 ± 5.6	1.1 ± 0.0
31. Hennhausi	2.74 ± 0.38	816 ± 46	0.8 ± 1.4	0
32. Honey moon	1.72 ± 0.06	871 ± 61	4.1 ± 5.2	0
33. Imperial	1.67 ± 0.09	864 ± 62	1.1 ± 0.0	0.6 ± 0.0
34. Jodoigne	2.46 ± 0.18	964 ± 52	1.1 ± 0.0	6.1 ± 3.9
35. Katalán	2.03 ± 0.18	870 ± 58	2.8 ± 4.4	1.1 ± 0.0
36. Kék tojás	1.81 ± 0.04	1179 ± 45	3.3 ± 0.0	0
37. Kék úri	2.17 ± 0.09	1162 ± 36	0	11.6 ±10.1
38. Késői muskotály	2.63 + 0.15	1083 ± 70	2.2 ± 0.0	0
39. Kirke szilva	2.44 ± 0.17	1154 ± 50	0	22.2 ±19.7
40. Korai kedvenc	2.50 ± 0.13	780 ± 27	0	0
41. Leppermann Emma	1.96 ± 0.13	1252 ± 17	1.7 ± 0.0	0
42. Letricourt	1.74 ± 0.07	882 ± 33	0	0
43. Lőweni szép	2.16 ± 0.08	943 ± 33	13.1 ± 4.7	16.1 +22.4
44. Mammut Dorota	1.99 ± 0.10	1092 ± 52	0	0
45. Milánói császár	2.28 ± 0.15	815 ± 12	0	0
46. Mirabellák királynője	2.47 ± 0.12	952 ± 60	2.2 ± 0.0	0
47. Montfort	2.52 ± 0.12	973 ± 52	0	0
48. Nagybányai Besztercei	1.86 ± 0.15	1204 ± 91	3.9 ± 8.0	0
49. Nagy cukor	1.77 ± 0.09	1248 ± 54	6.1 ± 9.5	0
50. Nagyherceg	2.32 ± 0.14	939 ± 32	0	0
51. Nancy ringló	2.40 ± 0.08	1040 ± 53	0	0
52. Olasz kék	1.89 ± 0.05	1149 ± 48	0	0
53. Ontario	2.56 ± 0.16	996 ± 41	0	3.3 ± 5.6
54. Pacific	1.54 ± 0.07	1333 ± 56	0	0.6 ± 0.0
55. Piros tojás	2.18 ± 0.20	1135 ± 23	2.2 ± 0.0	5.6 ± 1.2
56. Pond magonca	2.11 ± 0.09	1112 ± 19	10.3 ±18.8	8.9 ±11.5
57. Primate	2.60 ± 0.20	1284 ± 37	25.0 ±33.6	6.6 ± 5.8
58. Procureur	2.37 ± 0.18	1159 ± 42	13.6 ±14.7	0
59. Prugna d'Italia	1.96 ± 0.11	1008 ± 59	0	0
60. Ruth Gerstetter	1.87 ± 0.09	1180 ± 39	0	0
61. Sárga kajsziszilva	2.00 ± 0.11	1081 ± 66	4.7 ± 7.9	0
62. Sárga úri	2.73 ± 0.18	1175 ± 52	0	0
63. Sasbachi korai	1.65 ± 0.09	797 ± 34	0	0.6 ± 0.0
64. Sötétkék tojás	2.46 ± 0.20	983 ± 62	0	0
65. Szent Katalin	2.20 ± 0.09	1041 ± 40	0	0.6 ± 0.0
66. Szigeti zöld	1.78 ± 0.08	938 ± 37	0	0
67. Tarka perdrigon	2.19 ± 0.09	1221 ± 70	5.0 ± 5.2	0
68. Tragédia	2.15 ± 0.14	829 ± 53	0	0.6 ± 0.1
69. Toursi nagy	2.03 ± 0.29	995 ± 27	8.9 ±15.6	0
70. Uhinksz ringlója	3.13 ± 0.22	882 ± 86	2.9 ± 4.1	0
71. Vinke korai	3.47 ± 0.10	979 ± 57	1.7 ± 0.0	0
72. Violaszínű perdrigon	2.30 ± 0.20	815 ± 48	1.7 ± 0.1	0
73. Violaszínű ringló	1.81 ± 0.04	1247 ± 40	6.8 ± 6.6	0
74. Vörös nektarin	2.11 ± 0.04	1091 ± 30	0	0.6 ± 0.0

Table 14 (cont.)

Variety	Relative stamen number n/mm	Stigma diameter µm	Apistilly %	Polycarpy %
75. Vörös szilva	2.47 ± 0.14	872 _ 52	1.1 ± 0.0	0
76. Walesi herceg	2.10 ± 0.10	1245 ± 25	24.2 ±28.7	0
77. Wangenheimi	2.43 ± 0.13	1084 ± 64	2.2 ± 0.0	3.3 ± 0.0
78. Waschmann Berta	2.10 ± 0.21	890 ± 27	30.3 ±16.1	0
79. Washington	2.21 ± 0.16	1146 ± 82	1.7 ± 0.0	2.8 ± 4.4
80. Zöld ringló	2.26 ± 0.08	933 ± 20	2.8 ± 3.9	0.6 ± 0.0
F-value	15.33	620.70	46.40	49.22
SD 5%	0.11	17.95	1.72	2.60
SD 1%	0.15	23.72	2.28	3.44
SD 0.1%	0.19	30.32	2.91	4.40

tion of the year is very conspicuous in the pollination experiments. For the greengage Althann the Besztercei plum variety, and for the Debreceni muscat the Olasz blue are reliable pollen donors, but e.g. the pollinator varieties of the Zöld greengage trees were found to be unreliable. A comparison of the Italian and Hungarian results emphasizes the role of the site conditions,too (Table 12).

The heights of stigma related to the anthers - as mentioned in the introduction - do not give sufficient explanation of the self-fertile and self-sterile nature of the varieties. Low and high position stigmae are equally found in both fundamentally different variety groups, irrespective of the disposition to self-fertility, which is also explained by the positive correlation between pistil length and stamen length. The Chi^2 value is very low, that is, the relative heights of stigma and anthers are in no causal relation with self-fertility (Table 13).

Disposition to self-fertility is mainly correlated with the relative number of stamina. In the slightly feminine Besztercei plum the higher relative number of stamina is unfavourable for the potential fertility, while the feminine flowers of the masculine Montfort variety ensure the morphological bases of a better self-fertility.

The extent of self-fertility and certain morphological data and the nature of their correlation equally point to a year dependence; it can be supported by our own investigations and with the results published in the relevant literature. Accordingly, from the point of view of self-pollination

the relative stamen number,

the stigma diameter and

the varieties' disposition to apistilly and polycarpy

are the most important morphogenetic characters (Table 14). However, they show dynamical changes and demonstrably influence the prosepcts of fertilization.

The basic morphological characteristics of the 80 plum varieties examined are summed up in Table 14, where fluctuations in the 6 years are also expressed - by the scatter of the mean values. As seen in the table the relative stamen number ranges from 1.36 to 3.47 n/mm, which means an average of 2.20/mm. The average stigma diameter of the cultivated and historical plum varieties is 1008.9 μm, the extreme values are: 777 and 1333.

In many plum varieties neither apistilly nor polycarpy occur in the flowers, while there are certain varieties in which either one or the other teratoma, or even both of them are frequent, characteristically of the variety.

The following varieties are characterized by a large number of deficient flowers: Ageni 2, Burdett Angelina, Csúcsos szilva, Lőweni szép, Pond magonca, Primate, Procureur, Prince of Wales and Waschmann Berta. Polycarpy mostly occurs in the varieties Kék úri, Kirke szilva and Lőweni szép (Table 14).

As mentioned in the literary review the morphological studies of flower in plum varieties by DAHL (1935), RÖDER (1940) and TÓTH (1957) are regarded as standard works. A comparison of th mentioned authors' results with our own data was published in an earlier work (cf. SURÁNYI, 1985b). With possible differences in the method of sampling, the varieties examined, and the modifying effect of the sites taken into consideration, the measurements and ratios of the flower parts can be said to be very similar. Minor differences can be regarded as self-evident.

The relative stamen number, the stigma diameter as well as apistilly and polycarpy are morphological characters of basic importance from the point of view of self-pollination. Description of varieties on the basis of flower can be completed by further five characteristics.

To sum it all up, it can be said that the measurements and ratios of the reproductive organs are in correlative (competitive) relation with one another. The measurements of the different flower organs change not only in correlation with each other, they are also influenced by outer factors which modify the structural and functional conditions in accordance with the rule of those changes.

This new interpretation of the flower structure greatly facilitates the variety research, the breeding work (first of all the selection), and helps in evaluating the agrotechnical results.

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Acta Botanica Hungarica 35(1-4), pp. 227-236 (1989)

FLORAL NECTARIES AND NECTAR PRODUCTION OF SOUR-CHERRY CV. "PÁNDY" CLONES

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(Received: 20 November 1987)

Anatomy of nectaries of "Pándy" sour-cherry clones and their nectar secretion have been studied. 1) Green receptacular nectaries of Cerasus vulgaris Mill. cv. "Pándy" are found between the carpel and stamens slightly protruding from the inner surface of the receptacle. 2) Characteristic features of the glandular surface are the form of the epidermal cells, the crests and thickness of the cuticle. 3) Anomocytic stomata occur at the level of the epidermis or slightly sunk into it. Their presence and degree of their sunkness into the epidermis are characteristic to the clone. Clones vary also in the form of stomata. 4) Small cells of the glandular tissue with large nuclei constitute tangential rays. There is a close correlation between the size of the glandular surface of the receptacle (in longitudinal section) and the nectar secretion during the most productive periods. 5) The autofertile clone "Újfehértói fürtös" (P 2) has smaller glandular area and less nectar secretion than the autosterile ones. Clones with maximum production nectar during the evening and night hours (P 31, P 47, P 48) have the largest nectaries and the highest nectar production, but these - except the clone P 48 of rich nectaries - have been withdrawn from the large-scale farming, presumably, because of the disadvantageous characters for bee-pollination.

Introduction

Gardeners and bee-keepers find it particularly important to know the nectar secretion of the varieties and clones of fruit trees. This knowledge provides valuable data for the orchard gardeners to clarify insect pollination entomophilous fruits and to find reasons for inappropriate pollination and to help bee-keepers in forecasting honey yield.

Various species of Rosaceae were compared with other taxa (FELDHOFEN, 1933; BROWN, 1938; FAHN, 1953 and FREI, 1954) considering position and structure of nectaries with the intention of classifying them into a natural system. Recently, a number of researchers studies the description of higher natural groups based on the structure of nectaries (GULYÁS, 1988; GULYÁS and DARÓK, 1987).

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Nectar production of sour cherry varieties has been studied by several researchers (BEUTLER, 1930; VANSELL, 1952; LIVENTSEVA, 1954; SAZIKIN, 1955; RIMASHEVSKY, 1957; GLOWSKA, 1958; PELMENEV, 1969; SIMIDCHIEV, 1971; PÉTER, 1972) although very few of the Hungarian clones applied in large-scale farming (or destinated to introducing into it), were investigated (NIKOVITZ, 1980).

According to PÓR and FALUBA (1982) the honey yield value of various clones of sour cherries of the presumably Hungarian "Pándy" were determined by NIKOVITZ (1980).

Structure of nectaries and periodicity of nectar secretion of two clones (P 31 and P 114) have been presented by OROSZ-KOVÁCS et al. (1987a, b, and c). The knowledge of nectar production of the autosterile, entomophilous and inefficiently pollinating sour cherry clones (PÓR and FALUBA, 1982) may contribute to a more successful selection of taxa characterized by higher fruit yield, better pollination and more favourable insect-pollination, and furthermore, they can also help farmers in choosing autofertile clones.

Material and Method

Between the years 1983-1987 at Danitzpuszta state farm near to Pécs, under identical environmental conditions, on loamy calcerous clay, in a sour cherry orchard planted in 1969, nectar secretion of flowers in eight different Pándy clones were investigated. The studied clones were: P 2 ("Újfehértói fürtös"), P 5, P 10, P 31, P 38, P 50, P 114. Most of the late fruiting clones have been withdrawn from the large-scale farming and their further plantation is not allowed.

In spite of these measures these late clones have been chosen for our investigations especially for seeing a possible correlation between inefficient pollination and the unsufficient amount of nectar secreted. P 48 clones retained in large-scale farming was studied at Érd, "Elvira Plant" of the Firm for Fruit and Ornamental Plant Development, under circumstances completely different from the others described above. This is the reason, why for characterizing this clone we do not refer to the data of the more habitat-dependent nectar secretion but to those of nectary structure genetically more constant and less liable to environmental changes.

To study the glandular tissue structure, paraplastic embedding and colouration with toluidin-blue were used. Twenty flowers/clones were wtudied; measurements were made on five to ten sections/flowers. In the longitudinal section of the flowers length and width and surface size of the glandular tissue in the floral nectaries were measured. We found the glandular tissue approximately square-shaped to be of distinctive value. This parameter showed close correlation with nectar production.

Nectar production was measured in traditional way after a 24 hours' isolation using the method of DEMIANOVITZ and HLYN (1960). From earlier studies, however, we know that clones of Pándy sour cherries are not homogeneous regarding the periodicity of the nectar secretion, and passing over the production maxima, they often do not secret nectar anymore. Hence following the method of the above-mentioned authors, in our comparative study the average values of the nectar yields sampled during the secretion maxima, were used. In the present study data of

the year 1986 are provided, when samplings were taken of all the eight clones throughout the entire blossoming period in hour. Thirty measurements per clones were made during each secretion-maximum - their mean values are given below. For more details, see KOVÁCS, GULYÁS, and INHOF (1987), KOVÁCS, GULYÁS, SÜTÉT and HORVÁTH (1987), KOVÁCS, GULYÁS and HALÁSZ (1987).

When comparing nectar secretion of various clones sugar yield expressed in mg was regarded as basis calculated from the amount of nectar and its sugar concentration, with the following formula:

$$S = \frac{N}{100} : Dm\ \%,$$

where S: sugar value, N: amount of nectar in Mg produced by one flower: Dm %: dry matter.

The amount of nectar was determined with torsion scales, sugar concentration with ZEISS-ABBÉ refractometer.

During the samplings air temperature and relative humidity with psychrometer were registered.

Air temperature ranged between 7 and 30 ^{o}C, relative humidity from 45 to 87%. Correlations betweens nectar production and other parameters were pointed out in KOVÁCS, GULYÁS and INHOF (1987), KOVÁCS, GULYÁS, SÜTÉT and HORVÁTH (1987).

Results

BROWN (1938) and FAHN (1953) say that in the order Rosales, cup-shaped receptacular nectaries are situated between the stamens and ovaries. Nectaries of Cerasus vulgaris Mill. cv. Pándy are of an ancient type, they are green and cover the inner surface of the receptacle slightly protruding of it (Figs 1A, 2A,B,C,D). There are no great differences between the nine studied clones as regards colour and form of glands, but they differ in size.

The surface of the nectaries is smooth in the clones P 22, P 47 and P 114, and undulated in the others. The unevennesses of the surface can be usually found around the stomate impressed under the surface of the epidermis. Epidermis is covered by a cuticular layer. Cuticle forms a pattern of wrinkles and depressions which appears as small crests and valleys in cross-section. Wrinkles of the cuticule prevent unwanted flowout of the nectar. Thickness of cuticle is also characteristic to various clones: it ranges between 1.9 and 5.1 µm, P 38 has the thinnest, P 5 has the thickest one (Fig. 1), while the cuticle is thin in the clones P 2, P 10, P 48 and P 114.

The epidermis consists of one layer of cells. Its cells are slightly elongated, uniso-diametrical, mostly penta- and hexagonal, but some of them may be polygonal, too. Anticlinal walls are straight (Fig. 1E). Cells are of thon walls closely arranged and very small.

Unevennesses of the epidermis are increased by the hemisphaerically protruding tangential walls, moreover, on the outer tangential walls small elevations can be also observed, in the case of some clones as P 5, P 31, P 50 (Fig. 1C).

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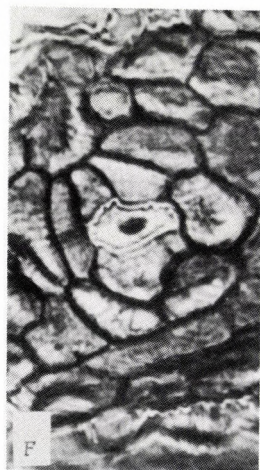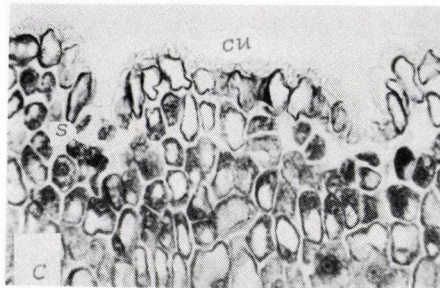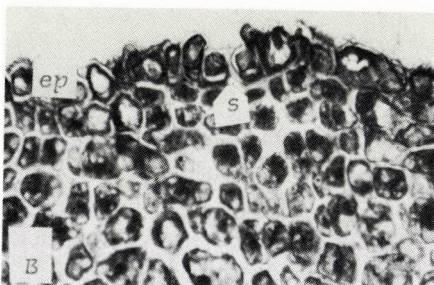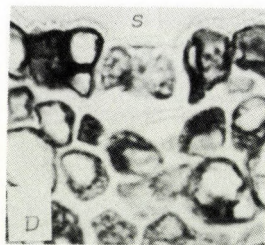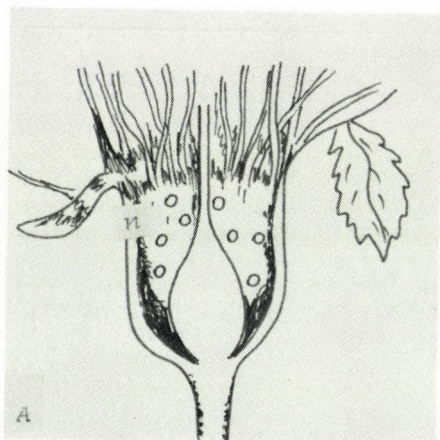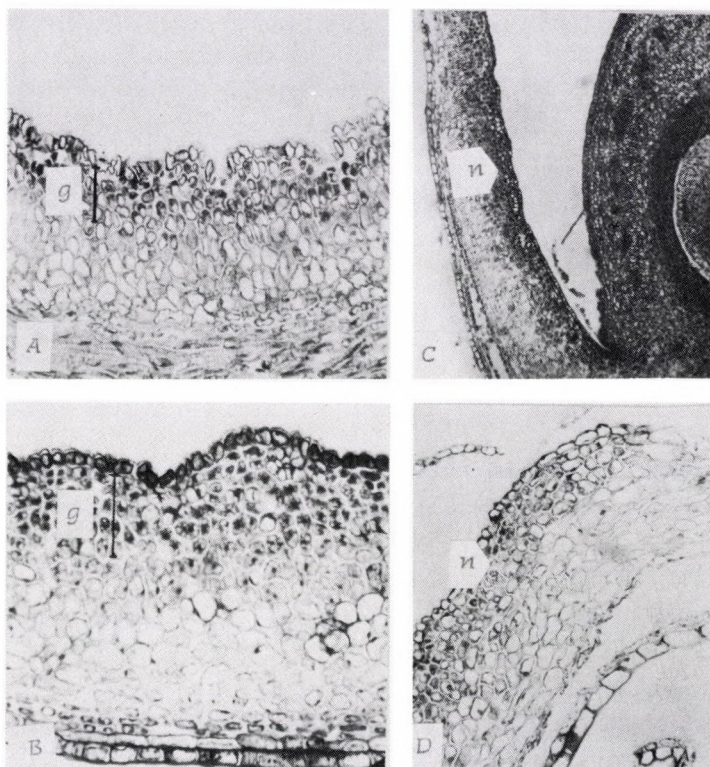
Fig. 2. Median longitudinal section of nectaries in different clones of Cerasus vulgaris Mill. cv. "Pándy"
A: Glandular tissue in the clone P 5 - B: and in the clone P 48 - C: nectary of the clone P 48, C: nectary of the clone P 48 - D: nectary of the clone P 2 protruding from the surface of the receptacle - g) glandular tissue - n: nectary

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Fig. 1. Cerasus vulgaris Mill. cv. "Pándy": surfaces of nectaries

A. Median longitudinal section of the flowers. - n: nectary
B. P 2 clone: stomata sunken till the middle of the epidermal cell layer. - s: stomata, ep: epidermis
C. Epidermis and sunken stomata of the nectary in the P 5 clone
D. Stomata in the level of the epidermal cells, in the clone P 2
E. Cuticle pattern of the nectary surface of P 2
F. Epidermis of the nectary with stomata in the clone P 2

There is a correlation between the data of width and length of the cuticular cells and those of the section of the nectaries (Table 1). The epidermis of the clones P 2 and P 48 have the smallest cells. The ratio length/width shows the form of the cells. Those having a ratio less than 1, are short high and oval shaped ones, like P 2, P 5, P 31, P 38, while in the other clones they have alongated parallelogram shape (Table 1).

Among the cells of the epidermis a large number of scattered stomata can be found. Nectar gets to the surface through the stomata. Closing cells are bean-shaped, they have no auxiliary cells. Stomata type are anomocytic, the number of surrounding cells is generally 5 (Fig. 1F). The form of the stomata can be classified as round (long./lat. = 1.-1.4; e.g. in P 5, P 10, P 38, P 47, P 48, P 50) and oval (long./lat. = 1.5-1.8, e.g. in P 2, P 31, P 114, see Table 1).

Stomata of the nectaries in few clones are situated in the epidermis level, they are sunken at most till the middle of the epidermal cells. In these clones nectaries have an almost even surface: P 2, P 47, P 114 (Table 1, Fig. 1A,D). The majority of the clones is characterized by sunken stomata: they can be found one, two and three layers (+, ++, +++) below the epidermis. Stomata of P 5 are sunken the deepest (Fig. 1C).

The clones P 22, P 38, P 48 and P 114, which are still used in the large-scale farming - have the epidermis of the nectaries covered b, a thin cuticle and slightly sunken stomata.

Glandular tissues, spread under the epidermis constituting broad lines, their smaller cells form tangential rays parallel with the surface. Cells are closely connected without intercellular space. In the cells of the glandular tissue nuclei are large - expressing a higher intensity of metabolism (Fig. 2A,B). Vessels of the receptacle run parallel with the glandular tissues, they do not spread branches towards the glandular tissue, so the nectaries are not provided by vessels.

There is a clear correlation between the size of the glandular tissue (measured in longitudinal section of the flower) and the nectar production measured during the periods of the secretional maxima, - as it is proved by the values of the linear regression (Table 2, Fig. 3). Production data obtained after the 24 hours' isolation cannot be used for comparison because of the different dates of the secretional maxima (KOVÁCS, GULYÁS and HALÁSZI, 1987).

Data in Table 2 show that even 40% of difference may exist between the volumes of flower nectaries of sour cherry clones (P 48 and P 5).

Table 1

Data of nectaries epidermis of Pándy sour cherry clones

(based on 100 measurement/clone)

Clones	Thickness of cutide	Epidermal cell			Stomata			
	µm	L µm	W µm	L/W	sunken	L µm	W µm	L/W
P 2	2.56	14.34	13.44	1.06	-	20.48	11.52	1.77
P 5	5.12	18.31	18.05	1.01	+++	26.88	19.2	1.4
P 10	2.42	14.59	19.46	0.74	++	28.16	25.6	1.1
P 31	3.84	19.58	18.69	1.04	+	26.88	16.64	1.62
P 38	1.92	20.22	18.56	1.08	+	30.72	27.62	1.12
P 47	3.21	21.38	16.89	1.26	-	26.08	25.6	1.02
P 48	2.54	16.38	12.93	1.27	+	29.44	27.14	1.08
P 50	3.33	19.2	23.04	0.83	+	25.6	23.04	1.11
P 114	2.05	19.5	12.87	1.49	-	26.42	16.69	1.58

Index: - : no sunken stomata
+ : stomata below epidermis, one cell depth
++ : stomata below epidermis, two cells depth
+++ : stomata below epidermis, three cells depth

L : length
W : width

Table 2

Size and secretion of nectaries

Clones	Size of nectaries			Nectar secretion						
						secretion period		24 hours isolation		
	L µm	W µm	L x W mm^2(X)	Gl.t number of cell layers	maximum nectar mg	sugar %	sugar mg(Y)	nectar mg	sugar %	sugar mg
P 2	2960.06	60.66	0.1795	3.8	1.96	21.09	0.4134	5.63	19.59	1.1032
P 5	2821.92	52.29	0.1475	3.15	1.57	19.86	0.3118	2.32	27.9	0.6473
P 10	3188.62	74.37	0.2371	4.48	2.27	22.04	0.5017	5.07	21.88	1.1093
P 31	3112.97	78.43	0.2441	4.73	2.32	23.52	0.5456	5.02	28	1.456
P 38	3030.53	69.31	0.21	4.17	1.75	35.45	0.4453	3.41	25.5	0.8695
P 47	3241.84	71.79	0.2327	4.33	1.73	24.83	0.4296	2.29	25.58	0.5857
P 48	3080.4	96.18	0.2965	5.8						
P 51	2837.04	69.17	0.1962	4.16	1.77	22.08	0.3909	2.81	35.85	1.0073
P 114	3040.44	73.84	0.2082	4.45	1.79	29.26	0.5237	3.03	30.23	0.9159

Clones underlined are still present in large-scale

Index: L: length; W: width; Gl.t: glandular tissue
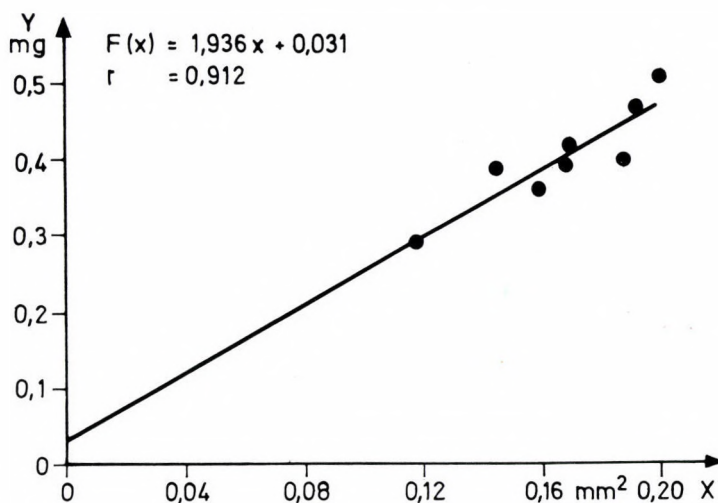
Fig. 3. Correlation between the surface of glandular tissue (in square mm) and the sugar value of nectar produced (in mg)

It is well-known that larger glands allways produce a higher amount of nectar. This surplus rises to 33% during the secretional maxima, and in a single flower it can reach 54% during a day. We can conclude of these data that there is a wide range of variance in the nectar production of various clones.

Autofertile "Újfehértói fürtös" (P 2) has much less of nectar production and smaller size of glandular tissue than the autosterile clones (KOVÁCS, GULYÁS and HALÁSZI, 1987). It can be established that the clones P 31, P 47, P 48, are the best nectar-producers, with production maxima in 6, 12, 18 and 24 hours, having their active periods in the hours of night and crepuscule. Among these clones we can find an only exception, the clone P 5. Except P 48, all the clones treated above had been withdrawn from cultivation. Among these clones disadvantageous from the viewpoints of bee-culture, P 48 has the thickest and largest glandular tissue. This motive makes necessary further investigations.

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Acta Botanica Hungarica 35(1-4), pp. 237-244 (1989)

PERIODICITY OF NECTAR PRODUCTION OF SOUR CHERRY CV. "PÁNDY"

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(Received: 20 November, 1987)

Periodicity of nectar secretion has been studied on eight clones of Cerasus vulgaris cv. "Pándy" every hour within identical ecological circumstances, from the early stage of blossoming until the latest one. Results: Nectar is produced every six hours in close correlation with the ripening stage of the genital organs, pistil secretion and pollen spread. Based on the periodicity of nectar production maxima clones can be divided into three groups: A: with nectar secretion at 3, 9, 15, 21 o'clock; B: with nectar maxima at 4, 10, 16, 22 o'clock, and C: with nectar peaks at 6, 12, 18, 24 o'clock. Stigma secretion easily evaporates in the warm mid-day hours, therefore the morning hours at 9 and 10, furthermore the early afternoon hours at 15 and 16 o'clock seem to be the most favourable for a successful bee pollination. The group C is unfavourable for pollination. They can be selected based upon their nectar secretion rythm in their early age of development, otherwise appropriate pollinating agents should be provided.

Introduction

It is particularly important to know the nectar production of the entomophilous flowers in autosterile species and clones. In the case of periodical nectar secretion bees are not provided with nectar during every period of the day. Therefore, it is reasonable to study various fruit species and sorts, wheather their nectar production would be abundant enough for the pollinating bees in the early spring, when they visit the blossoming flowers only for a short period of the day. BENEDEK and MARTINOVICH (1971) affirm that in the case of allofertile "Pándy" sour cherries practically no fruit can be expected without pollinating activity of bees. Because of the early blossoming of sour cherries the number of wild pollinating insects is fairly limited. Depending on the weather bees appear in blossoming cherry orchards between 9 and 10 o'clock, and do nto stay later than 16 o'clock p.m., except particularly warm days. Nectar production, in a great majority of plants is periodical. Its rhytmic appearence was recognized as early as in the last century, but it was not thoroughly studied until the late 1920-es. DOLGOVA

(1928), BEUTLER (1930, 1953), BOETIUS (1948) and MAURITIO (1960) described that plants secrete nectar only during a particular period of day and the maximum production may vary in the different species.

LÜTTGE (1971) supposes a hormonal regulation of nectar secretion. He supports his statement with argument that, in the majority of plants, the nectar secretion peaks are correlated to the development and ripening of the pollen and ovula.

Daily periodicity of nectar production in several so sour cherry clones have been studied by SIMIDCHIEV (1971). He took samples every two hours during the day and observed that between 6 o'clock p.m. to 6 o'clock a.m. a considerable amount of nectar was produced during the night. He described the rythmic changes of nectar secretion in sour cherries although he was unable to identify the production peaks by taking samples each second hours.

PESTI (1976) studied the daily rhythm of nectar secretion in Compositae species and he stated that the periodicity is of endogenous origin. It practically not influenced by any environmental factors. The daily rhythm is a feature characteristic for subfamilies.

Nectar secretion dynamics of two clones of sour cherry, "Pándy" 31 and 114, has been reported by OROSZ-KOVÁCS et al. (1987a, b). They described that sour cherry clones produce nectar in every sixth hours, and this activitiy is closely related to the maturity of the carpels and stamens, to stigmata secretion and pollen spread. Since the nectar production peaks in the two clones were different, this fact suggested the necessity of making studies on further clones for fruitgrowing and bee-farming pruposes.

Material and Method

On the fields of the state farm, Pécs, at Danitz, between 22 and 25th April nectar secretion of eight clones of Pándy sour cherries were sampled in each hour during the whole flowering period, under identical circumstances. The orchard was planted in 1969, on loamy clay. Clones studied were: P 2 ("Újfehértói fürtös"), P 5, P 10, P 31, P 38, P 47, P 50, P 114 ("Késői Pándy"). From these P 2, P 38 and P 114 have been retained in large-scale farming, the others, because of their incomplete fertilization, have been eliminated.

Sampling of nectar production was carried out following the method by DEMIANOVITCZ-HLYN (1960) with microcapillary glas-tubes from marked flowers (30 flowers/clones/hour, producing 1080 data each hour). The amount of the nectar and its sugar content were measured throughout a period 36 hours. The average data of these measurements are shown in Table 2. Sugar content was calculated using the following formula:

$$\text{Sugar mg} = \frac{\text{nectar mg}}{100} \cdot \text{sugar \%}$$

Table 1

Characteristic data of the nectary-epidermis in "Pándy" sour cherry clones

(n = 20 flowers)

Clones	Thickness of cuticle µm	Length of epidermal µm	Width µm	Length/Width	Submergency	Length	Width	Length/Width
		cells				of the stomata		
P 2	2.56	13.44	13.44	1.00		20.48	11.52	1.77
P 5	5.12	18.31	18.05	1.01	+++	26.88	19.2	1.4
P 10	2.42	14.59	19.46	0.74	++	28.16	25.6	1.1
P 31	3.84	19.58	18.69	1.04	+	26.88	16.64	1.62
P 38	1.92	20.22	18.56	1.08	+	30.72	27.62	1.12
P 47	3.21	21.38	16.89	1.26	-	26.08	25.6	1.02
P 48	2.54	16.38	12.93	1.27	+	29.44	27.14	1.08
P 50	3.33	19.2	23.04	0.83	+	25.6	23.04	1.11
P 114	2.05	19.5	12.87	1.49	-	26.42	16.69	1.58

Symbols: - stomata not submerged in the epidermis below the surface
+ stomata submerged to 1 cell depth
++ stomata submerged to 2 cell depth
+++ stomata submerged to 3 cell depth

Table 2

Size and production of the nectaries in "Pándy" sour cherry clones

Clones	Size of nectaries				Nectar production					
	Length	Width	Surface		at time of maximal production			24 hours isolation		
	µm	µm	mm^2		mg	sugar %	sugar mg	mg	sugar %	sugar mg
P 2	2960.06	60.66	0.1795	3.8	1.96	21.09	0.4134	5.63	19.59	1.1032
P 5	2821.92	52.29	0.1475	3.15	1.57	19.86	0.3118	2.32	27.9	0.6473
P 10	3188.62	74.37	0.2371	4.48	2.27	22.04	0.5017	5.07	21.88	1.1093
P 31	3112.97	78.43	0.2441	4.73	2.32	23.52	0.5456	5.02	28	1.456
P 38	3030.53	69.31	0.2100	4.17	1.75	25.45	0.4453	3.41	25.5	0.8695
P 47	3241.84	71.79	0.2327	4.33	1.73	24.83	0.4296	2.29	25.58	0.5857
P 48	3080.4	96.18	0.2965	5.8						
P 50	2837.04	69.17	0.1962	4.16	1.77	22.08	0.3909	2.81	35.85	1.0073
P 114	3040.44	73.84	0.2082	4.45	1.79	29.26	0.5237	3.03	30.23	0.9159

The underlined clones are still in production

The mass of the nectar was weighted on a torsion balance, sugar concentration was measured with a refractometer.

Of the climatic parameters air temperature and humidity were determined with Assman-psychrometer. During the sampling air temperatures ranged between 7 and 28 °C, and relative humidity between 52 and 93 per cents.

Results

Based on previous studies (OROSZ-KOVÁCS et al., 1987a, b) it was found that nectar production of Cerasus vulgaris Mill. cv. Pándy clones is periodical during the day and nectar is produced also in the night and the early morning hours. During the observation made on clones P 31 and P 114, it was noticed that the daily nectar production shows a curve with four peaks. Nectar was secreted in each sixth hours in close correlation with the ripening stages of the carpels and stamens.

We suppose that during the growth of the anthers and the ripening of pollen grains nutrients transported to the flowers would fully utilized, and later, because of the maturity of the pollen, after the opening of the anthers, the use of nutrients becomes unnecessary and the surplus of the phloem liquid will be secreted through the nectary.

When describing the nectar production of P 31 and P 114, we understood the regularities of secretion, which turned to be valid for the other clones as well.

There is no nectary in the bud, material secreted in the young flowers is thin. Nectar production is the most intensive during the spread of pollen grains and that of pistil secretion. Sugar concentration of the nectars grows during the flowering period.

Between the two clones under study decisive differences are observed in the time of production peaks. In the P 31 the cycle of secretion begins at 6 o'clock and in the clone P 114 at 4 o'clock a.m.

The nectar production of the P 31 is disadvantageous as to bee-keeping because three production maxima of the four existing ones occur during the late dusk and night hours: 18, 24 and 6 o'clock, respectively. Bees can utilize nectar produced at 12 o'clock, when, in warm weather, the surface of the stigmata is fairly dry and there is little chance for the adhesion of the pollen grains. P 47 and P 5 (Fig. 1) have similar cycles. The latter two ones have been eliminated from large-scale farming, and it is likely that their unsuitability derives from inefficient bee-pollination and from disadvantageous nectar production.

22. IV. 1986

Beginning of flowering

Early stage of flowering

23. IV.

Bulk stage of flowering

25. IV.

End of flowering

P 38 Nectar mg

P 2 Nectar mg

P 47 Nectar mg

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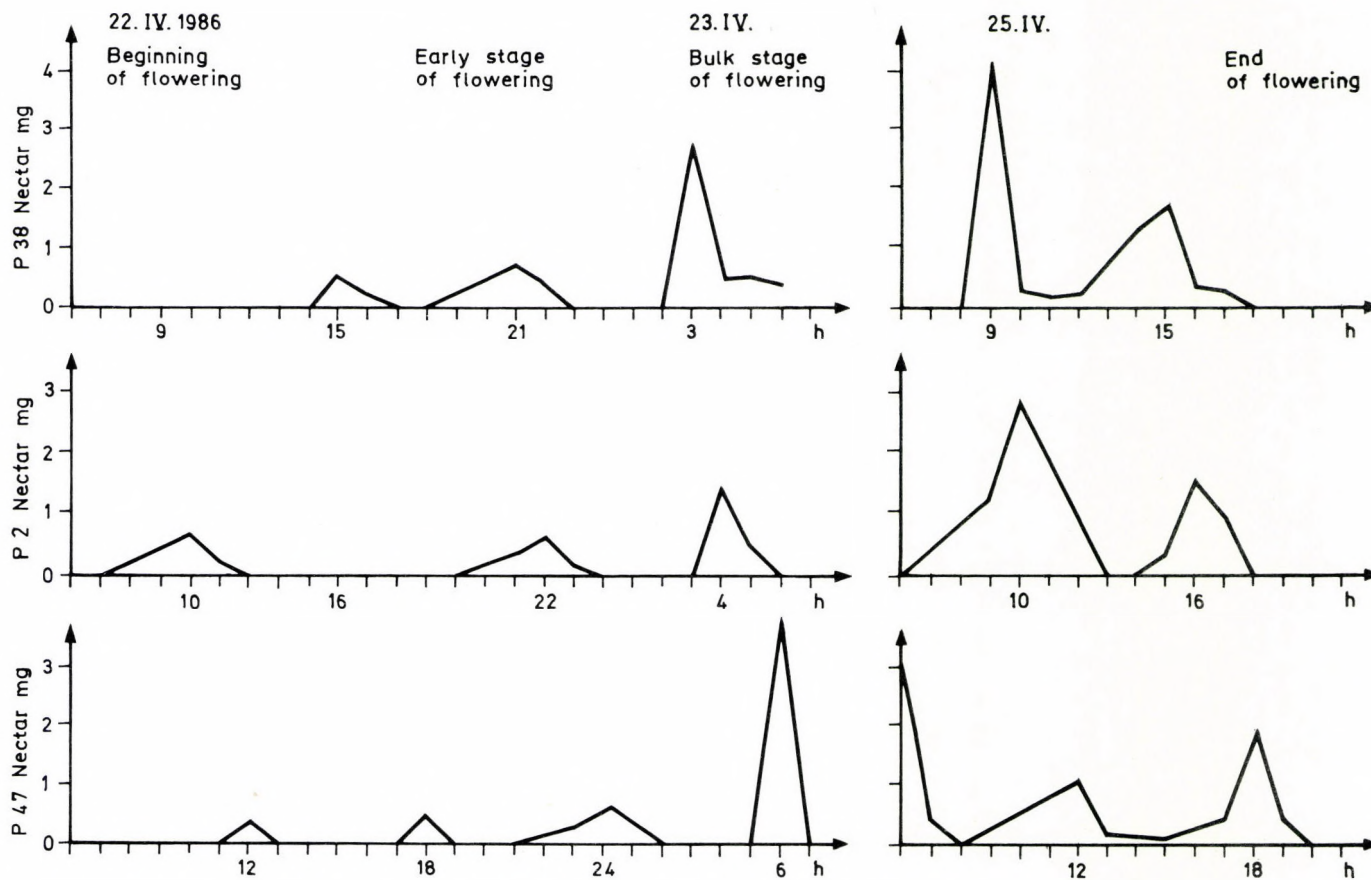
Fig. 1. Periodicity of nectar secretion in "Pándy" sour cherry clones

The daily nectar production of the P 114 begins at 4 o'clock a.m. During dusk and only two production peaks fall to the night hours. If the weather is favourable, at 10 a.m. and 4 p.m. bee-pollination may be successful. To this pollinating group belongs the so-called "Újfehértói fürtös" (P 2), the P 10 and the P 50 clones. The latter have nectar, bees frequent the insufficiently, thus they have also been eliminated from large-scale farming.

The third - so far undescribed - group is represented by the clone P 38. Its daily nectar production begins at 3 a.m. with secretion peaks at 9 a.m. and 15 o'clock, when more than half of the full daily amount of nectars is secreted. This is the third clone preserved in the farming.

Comparison of the periodicity of the nectar production with our flowering-biological observations revealed some correlations between the development of stamina and pistils. In the clone P 38 during the early blossoming stigma begins to shine at 15 o'clock and sinchronously the nectar secretion also starts. Not observing the flowers by night, anthers seem to open only one day later and thus, it can be supposed that between the maturation of pistils and anthers there is a one-day's delay at least. This is the reason why literature often considers sour cherries as protogynous (MALIGA-MOHÁCSI, 1956; NYÉKI, 1974).

In the clone P 2 the stigma secretion does not appear on the first day of blossoming and the flowers seem to be protrandric. Next morning, however, stigma secretes. The delay is twelve hours only, the lapse alteration is not significant, flowers are homogamous carpels and stamens work sinchronously though they seem to be proterandrous. Flowers of P 47 are also clearly homogeneous.

At the comparative structural evaluation of the nectaries of eight studied clones (O. KOVÁCS and GULYÁS, 1989) it was concluded that clones with the largest nectaries are the least valuable ones for bee-farming, having a 6, 12, 18, 24 o'clock cycle. Out of them only one single clone, P 48 has been retained in large-scale farming. Based on the aforesaid it seems to be confirmed that the Apis mellifica takes part in the pollination of those sour cherry clones exclusively in which secretion peaks occur in the morning and the early afternoon. Because, during blossoming, bees are collecting only in air temperatures over 10 ^{o}C. In the pollination of those clones whose flowers produce large amounts of nectar in the early morning and in the evening hours probably other wild species or eventually night insects have a role. In case we want to retain the valuable clones with

high yield but of insufficient bee-pollination, we have to resettle artificially pollinating insects into the orchards.

The daily rhythm of nectar production can be identified in the early blossoming of the samplings, thus, clones unsuitable for bee-pollination can be early selected and easily eliminated. Decads-long selecting work of fruit-producers can be reduced if clones disadvantageous from the viewpoint of nectar secretion will be removed in the samplings' period.

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Acta Botanica Hungarica 35(1-4), pp. 245-254 (1989)

DISTRIBUTION DEVELOPMENT AND STRUCTURE OF GUM-RESIN PRODUCING TISSUE SYSTEMS IN VATERIA INDICA L.

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Distribution, development and structure of gum resin producing tissue systems were studied in Vateria indica. Ducts are present in the leaf, root and pith of stem, while ducts and cavities are present in the secondary xylem of stem. Ducts in the leaf and the pith of stem develop schizogenously while the ducts and/or cavities in the secondary xylem of root and stem develop lysigenously. The presence of tylosoides in the ducts of the stem are also noteworthy.

Introduction

SOLERDER (1908) writes that "for the diagnosis of the order Dipterocarpeae a series of anatomical characters exists. Foremost among these is the possession of resin-canals". He further made an observation on the presence of resin-canals in Vateria but their course has not been traced nor their distribution. Since no information is available on the development, structure and distribution of duct system responsible for the exudation of gum, the present investigation was undertaken.

Vateria indica L. (Dipterocarpaceae) is a large evergreen tree indigenous to the evergreen forests. The tree is valued for its timber, 'resin' and tallow of the seeds. Resin exuded by the tree is known as Piney Resin, White Dammer or Dhupa. The essential oil in the resin shows marked antibacterial activity and hence this resin finds extensive use in Indian medicine (ANONYMOUS, 1986).

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Materials and Methods

Shoot apices, young and old stems, blocks of bark and wood from tree trunk, leaves and roots of V. indica were collected from trees growing in its natural habitats at Cochin, Kerala State, India, and fixed in FAA. Dehydration, infiltration, embedding in paraffin wax, sectioning and staining were done according to usual microtechnique procedures (BERLYN and MIKSCHE, 1976).

Results

Distribution of ducts and cavities

In young stem, ducts are present only in the pith and are distributed in a single row towards the periphery of the pith and opposite to the protoxylem of each vascular bundle (Plate I/1). A young stem has about 20-25 vascular bundles and an equal number of gum-resin ducts. These ducts are circular in outline, vertically elongated, continuous, parallel to the axis and do not anastamose with each other. Each leaf trace at the node is associated with a duct.

When the stem has about 1 cm deep secondary xylem, the ducts appear in secondary xylem also (Plate I/2). They are distributed at random with occasional grouping of 3-4 ducts in a tangential row, among the axial parenchyma cells. The xylem ducts are mostly circular in outline, vertically elongated, parallel to the stem axis or traverse obliquely. Adjacent ducts in a row anastamose tangentially, but a network of anastamosing ducts is not formed. The sylem ducts do not traverse the ray parenchyma. When the duct comes across a multiseriate ray it traverses obliquely along the tangential side of the ray (Plate I/3).

In addition to the ducts, several large cavities are also occasionally observed in the secondary xylem. The adjacent cavities of a row anastomose tangentially forming a network of cavities around the multiseriate rays (Plate I/4). As the cavities do not traverse the rays, the multiseriate rays appear as intact islands amidst the cavities.

Tyloses are absent in the vessels of young branches, but they are frequent in old stem after the formation of gum-resin ducts in the xylem (Plate I/5, 6). Tyloses often contain phenolic substances and sometimes they are heavily loaded with them (Plate I/6).

In petiole and mid vein, several ducts are distributed in the ground tissue inner to the vascular system (Plate II/1). The ducts are continuous
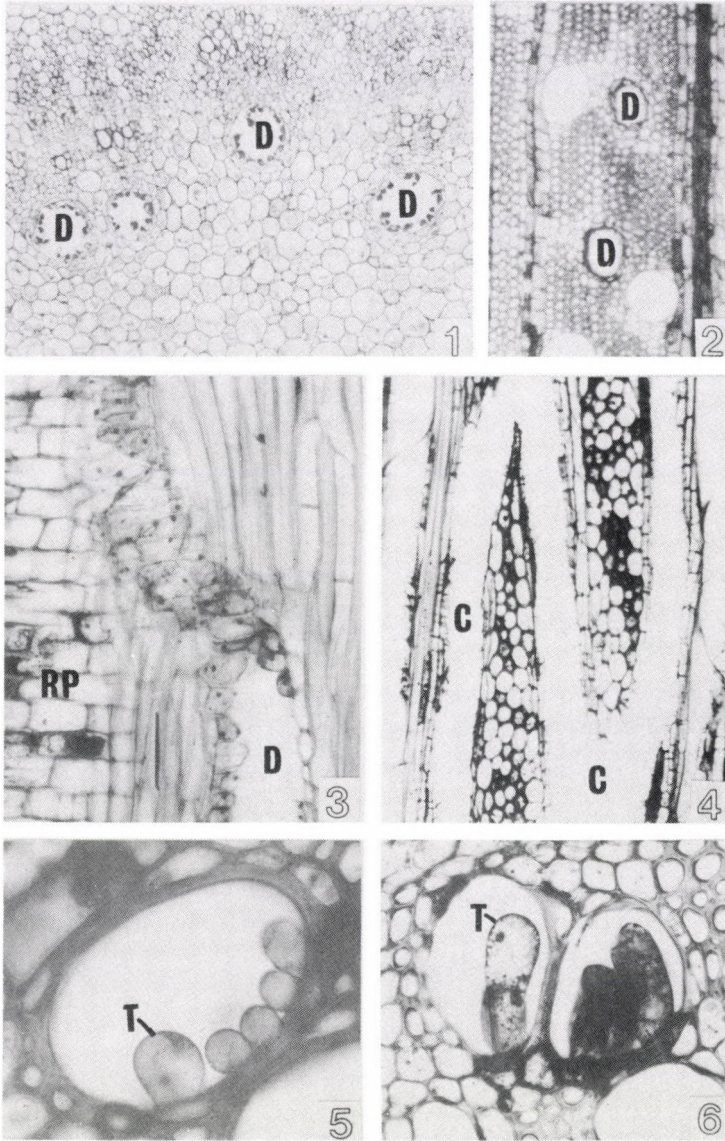
Plate I

1. T.S. young stem showing the pith ducts. x 40. - 2. T.S. The ducts distributed at random in the secondary xylem of stem. x 55. - 3. R.L.S. A duct traversing obliquely along the tangential side of the multiseriate ray. x 130. - 4. T.L.S. Tangential anastamosis of cavities around the intact multiseriate rays. x 140. - 5, 6. Tyloses in the secondary xylem. Some tyloses are filled with phenolic contents. x 540. (C, Cavity; D, Duct; RP, Ray Parenchyma; T, Tyloses)
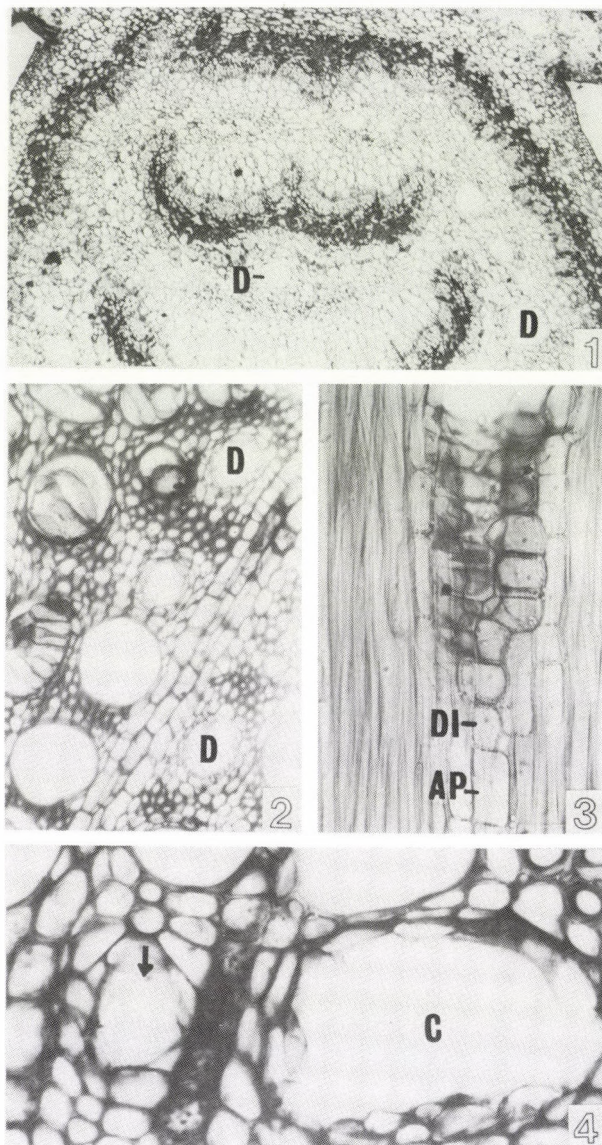
Plate II

1. T.S. Leaf trhough mid-vein showing several ducts in the ground tissue. x 55. - 2. Root showing ducts in the secondary xylem (Note the abundance of tyloses). x 55. - 3. R.L.S. Secondary xylem. The ducts initials are being formed by the transverse divisions of axial parenchyma cells. x 170. - 4. T.S. Formation of a cavity by the lysis of initials in the secondary xylem (arrow). x 500. (C, Cavity; D, Duct; DI, Duct Initial; AP, Axial Parenchyma).
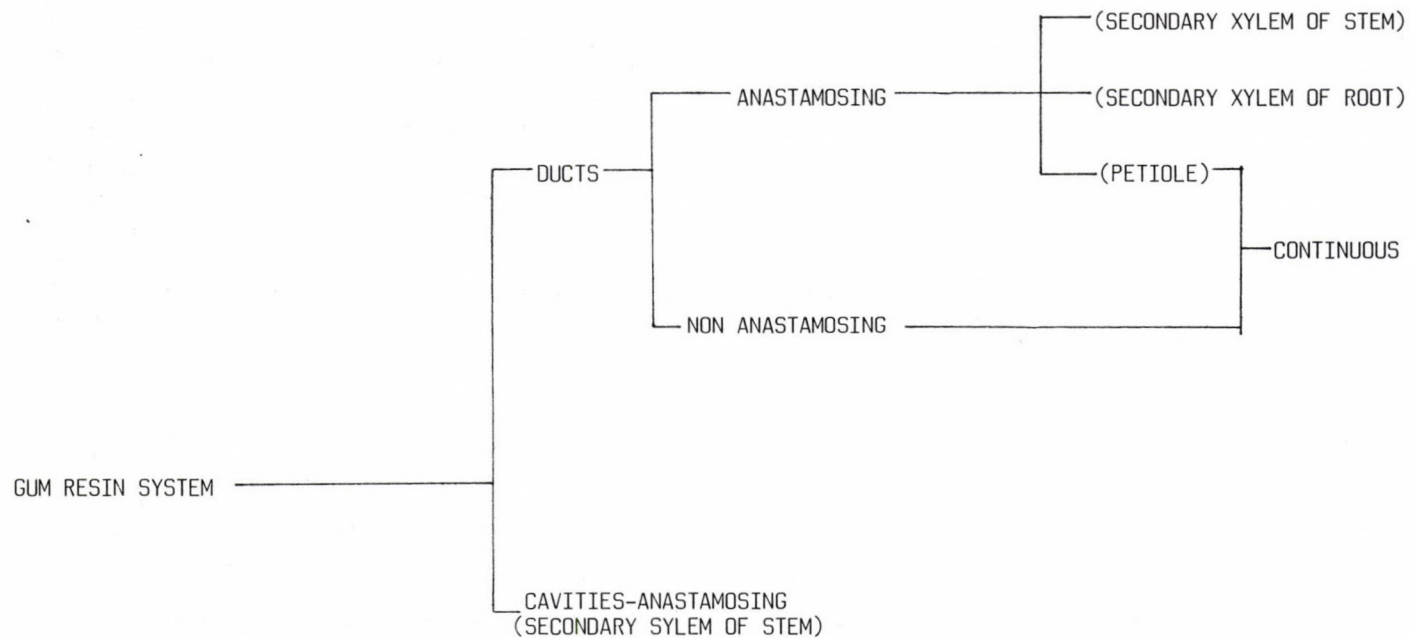
Fig. 1. The gum-resin system in *Vateria indica*
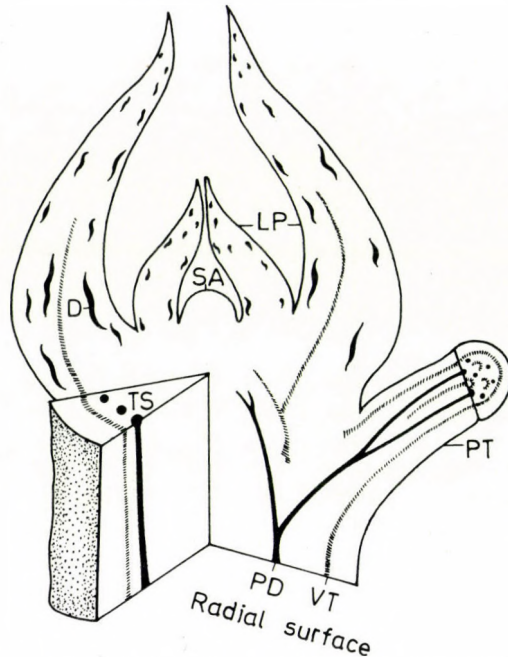
Fig. 2. A 3-dimensional representation of stem apex showing the distribution of gum-resin ducts. - (D, Ducts; LP, Leaf Primordia; PD, Pith Duct; PT, Petiole; SA, Stem Apex; TS, Transverse Surface).

throughout the leaf and all ducts of the mid-vein unite at the base of the petiole (see Figs 1 and 2). The lateral veins have a single duct each in the centre of the vascular bundle which is connected to a duct of the mid-vein. Thus, a continuity of duct system is established between the stem and the leaf.

In young roots, ducts and tyloses are absent. But after secondary growth, the ducts appear in secondary xylem and tyloses also develop extensively (Plate II/2).

Initiation of ducts and cavities

The ducts initiate schizogenously in the pith of the stem and leaf.

The ducts and/or cavities in the secondary xylem of stem and root develop lysigenously from the axial parenchyma cells.

A few axial parenchyma cells divide transversely forming a group of thin walled initials with prominent nuclei (Plate II/3). Lysis of these cells leads to the formation of a lumen (Plate II/4). The ducts then elon-
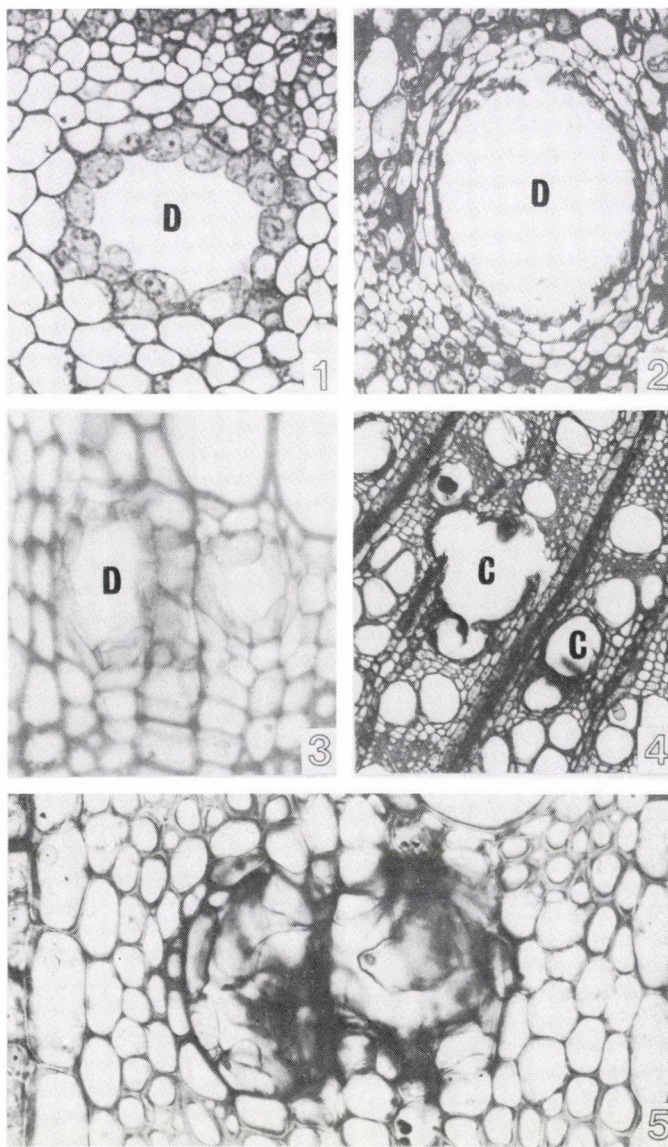
Plate III

1. T.S. Young stem just below the stem apex showing a pith duct. The distinct epithelial cells of the pith duct are contiguous. x 375. - 2. T.S. Pith duct in the old branch. The duct is surrounded by a few layers of sheath cells (Note the absence of distinct epithelium) x 200. - 3. T.S. Secondary sylem showing two gum-resin ducts. The ducts are lined by a distinct epithelium. x 200. - 4. T.S. Showing the gum-resin cavities in tangential view. Cavities are not uniform in outline and lack definite epithelium. x 130. - 5. T.S. A xylem duct filled with tylosoides. x 220. - (C, Cavity; D, Duct)

gate vertically due to the development of more initials from the axial parenchyma cells and their lysis.

The cavities develop as the lysis of axial parenchyma cells continues vigorously in vertical and tangential directions. All axial parenchyma cells between the adjacent ray breakdown forming a network of tangentially anastamosing cavities around the intact rays (Plate I/4).

Structure of the ducts and cavities

In young stem just below the stem apex, the pith ducts are bordered by distinct epithelial cells with large nuclei and dense cytoplasm (Plate III/1). In lower internodes some of the epithelial cells of the pith ducts undergo lysis followed by the disappearance of nucleus and darkening of the cytoplasm (Plate I/1). The epithelial cells which are previously contiguous separate at radial walls and subsequently they get detached to the duct lumen.

The pith cells around the ducts undergo periclinal divisions forming a few layers of tangentially flattened sheath cells around the ducts (Plate III/2). When the epithelial cells disintegrate, the sheath cells do not appear to simulate the epithelial cells in morphology, and consequently the pith ducts of an old stem are without a distinct epithelium (Plate III/2).

The ducts in the secondary xylem of the sem and root have a sharp boundary of epithelium (Plate III/3).

The cavities in the secondary xylem of the stem differ from the ducts in their irregular outline and absence of epithelium (Plate iII/4). Due to extensive lysis of axial parenchyma cells, often the cavities occupy a wide area between the adjacent multiseriate rays.

In stem, often epithelial cells proliferate into the duct and block the lumen (Plate III/5). Such structures are known as tylosoids which are characteristic of Dipterocarpaceae (CHALK, 1983). The tylosoids differ from the tyloses in that they are proliferations of thin walled epithelial cells and do not pass through any pith cavity.

Discussion

In the stem of Vateria indica, gum-resin ducts are present in the pith, while ducts and cavities are present in the secondary xylem. While the ducts or cavities anastamose tangentially sometimes forming a network,

their pith ducts do not anastamose and they run parallel to each other as in Terminalia crenulata (SETIA, 1976) and Bosewellia serrata (SUBRAHMANYAM, 1981). The distribution pattern of ducts varies in different tissues. The function of the exudates in the ducts and cavities could be peripheral protection against insect pathogens (DELL and McComb, 1978) or dessication (KRAMER and KOZLOVSKI, 1979). But the pith being an internal tissue, the aspect of peripheral protection does not arise and presumably, hence their anastamosis is absent. The pith ducts appear to be active only in the young stem before the development of ducts in secondary xylem. When the tip of an young stem is cut off, the resin oozes out and soldifies over the exposed surface of the stem. In young stem thus the pith ducts may serve for sealing and protection of injuries when the xylem ducts are not developed.

Continuity of ducts from the stem into leaf is also observed in many other plants, viz. Bozwellia serrata, Garuga pinnata (SUBRAMANYAM, 1981), Ailanthus excelsa and Lannea coramandelica (VENKAIAH, 1982). In V. indica a continuous duct system is maintained with the stem and the whole leaf. When we consider that the gum-resin is produced by the epithelial cells surrounding the duct, the significance of such an elaborate continuous system is not obvious. Probably such a continuous system facilitate the exchange of gum-resin or its precursors between the photo synthesizing leaf and the stem.

The gum-resin ducts in the pith and leaf of Vateria initiate schizogenously. Schizogenous development of duct is common in members of the family Anacardiaceae (FAHN and EVERT, 1974; NAIR et al., 1983; VENKAIAH and SHAH, 1984).

Cavities and ducts in secondary xylem of stem and root develop lysigenously as in Sterculia urens (SHAH and SETIA, 1976), Mangifera indica (JOEL and FAHN, 1980) and Ailanthus excelsa (BABU et al., 1987).

Eventhough the initiation of ducts is schizogenous, lysis of some epithelial cells is always observed during the continued duct development. Hence their total development is schizo-lysigenous. (Incidentally, CURTIS and LERSTEN (1986) investigated the bicellular foliar secretory cavities of Eupatorium rugosum and since the cavities develop neither lysigenously nor in true schizogenous fashion, they proposed the term 'pseudoschizogeny'.) Ducts are initiated schizogenously in the primary and lysigenously in the secondary tissue. There is no consistency in the manner of duct initiation even in different tissues of the some organ of the plant. A similar situation is observed in Lannea coromandelica (VENKAIAH and SHAH, 1984), where

ducts develop schizogenously in the primary phloem, pith and sylem rays, and lysigenously in the secondary phloem and phelloderm.

Acknowledgements

Thanks are due to D.S.T., New Delhi for financial assistance.

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Acta Botanica Hungarica 35(1-4), pp. 255-260 (1989)

REACTIVATION OF THE DORMANT LENTICELS IN TWO HIMALAYAN TREE SPECIES BY THE EXOGENOUS APPLICATION OF STIK* AND GA_3

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The cuttings of Holoptelia integrifolia and Pyrus pashia trees receiving STIK as well as GA_3 at 0.1, 0.2, 0.5, 1.0 and 2.0 $mgml^{-1}$ levels showed that the stimulation of lenticels is more or less parallel in the two taxas. The percentage induction in number of lenticels in H. integrifolia for each concentration of STIK and GA_3 was higher than that of P. pashia. However, the latter species showed a pronounced response for both the growth regulators in increasing the area of the lenticels. The higher concentrations of STIK proved more effective in inducing the initiation of new lenticels, whereas GA_3 showed pronounced influence at lower concentrations.

Introduction

A vast majority of species that form periderm also produce lenticels in the various parts of the plants including roots, shoots, as well as the fruit walls. Only a few reports are available concerning the primary nature of the lenticels, as modified by IAA and GA_3 treatment, either alone or in combination, on the aerial shoots of some woody plants (GHOUSE and YUNUS, 1974; AHMAD and MATHEW, 1979; BADOLA, PALIWAL, S.P. and PALIWAL, G.S., 1983). The effect of Niagara on the dormant lenticels of Cedrella toona was in addition a new report by us besides the confirmation of known results of the above two hormones (BADOLA, PALIWAl, S.P. and PALIWAL, G.S. (1983).

In the present communication we have selected two trees, viz. Holoptelia integrifolia and Pyrus pashia from different altitudes (560 m and 1500 m, respectively) and found that they show a more or less parallel response to the various concentrations of STIK and GA_3. Till now, there is no

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*Commercial name for the biologically active substances comprising naphthalene acetic acid, sodium salt and inert ingredients, sponsored by FMC Corporation, Agriculture Chemical Group, Philadelphia (USA), with the Code No. 551.

Akadémiai Kiadó, Budapest

published work on the effect of STIK (which bears the active ingredient nephthalene acetic acid with sodium salt), a new plant growth regulator, on the lenticels.

Materials and Methods

The effects of STIK and GA_3 at the concentration levels of 0.1, 0.2, 0.5, 1.0 and 2.0 $mgml^{-1}$ have been observed on the one year old stem cuttings of approximately equal thickness and length (20 cm) from the trees, viz. H. integrifolia and P. pashia during the period middle of December to middle of February. The cuttings were grouped into batches of 25 each. Their basal ends were dipped in aqueous solutions of different concentrations of the hormones, separately, to a depth of 5 cm for 48 hrs at the room temperature (13 $\pm$ 1 ^{o}C). Distilled water treated sets served as the controls. All the cuttings were then placed upright in the soil pots (20 cm in diameter), containing garden soil and kept under laboratory conditions (9 to 17 ^{o}C). The upper ends of the twigs were wrapped with moist cotton to avoid drying. Nearly 10 cm part below 1.5 cm of each cutting from the upper cut surface was marked with India ink and considered for observations (number and size, etc.). The lenticels which show revival of activity become slightly raised above the surface of the bark and appeared light cream in colour, as a result of production of additional complementary cells, due to the activity of groups of lenticel meristem.

Observations

The results have been given in Figs 1 and 2. The stem cuttings maintained as 'control' did not show any significant change in the number, area, and the colour of lenticels. On the other hand, the samples receiving different growth regulators experienced alterations in all these features and appeared as prominent, light-creamy lesions, indicating a positive response to various treatments.

In all the concentrations of STIK, the percentage increment in the number of lenticels is higher in H. integrifolia than that of P. pashia. However, the general pattern of percentage increment in the number is similar for both the species for all the concentrations of the two hormones tested. Furthermore, although the percentage increment in the number is higher in H. integrifolia than that of latter taxa also for all the concentrations of the STIK. The area gives a picture different from the number. P. pashia shows a much higher response than that of the former taxon both for STIK and GA_3, though the difference is little for STIK than GA_3 between the two taxa. For STIK, the percentage induction in the number of lenticels gradually increases from 0.1 $mgml^{-1}$ to an optimum of 1.0 $mgml^{-1}$ concentration, and then declines to 2.0 $mgml^{-1}$ level for both the taxa.
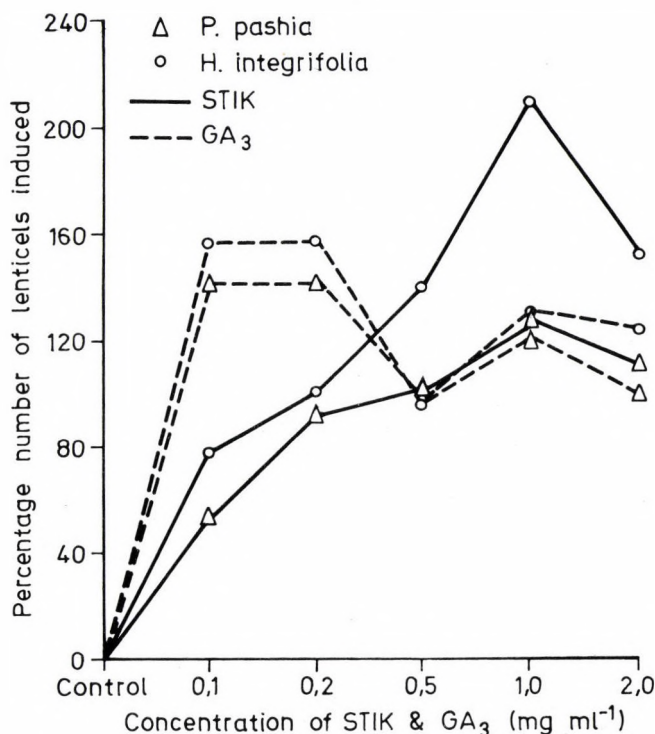
Fig. 1. Augmented number of lenticels after treatment with different concentrations of STIK and GA_3 supplied as aqueous solution in H. integrifolia and P. pashia

In general, the higher concentrations of STIK were more stimulatory in inducing the initiation of new lenticels.

GA_3 has shown a different trend. Here, the maximum number of lenticel induction has been observed for GA_3 at 0.1 and 0.2 $mgml^{-1}$ levels, then it declines to its lowest value for 0.5 $mgml^{-1}$ treatment. It further increases slightly for GA_3 at 1.0 and 2.0 $mgml^{-1}$ levels.

The increment in the area of lenticels by STIK did not show any fixed pattern by increasing the concentrations but follows the same trend for both the taxa. The highest induction in the area has been observed by STIK at 0.1 and 1.0 $mgml^{-1}$ levels. However, GA_3 does exhibit a gradual pattern in the area change, it increases with an increasing concentration up to an optimum level of 0.5 $mgml^{-1}$, thereafter a decline has been observed for the higher concentrations. In general, STIK and GA_3 both had more or less equal effectiveness in breaking the dormancy of the lencticels.

Fig. 2. Increase of lenticel area after treatment with different levels of STIK and GA_3 supplied as aqueous solution in H. integrifolia and P. pashia

Discussion

The results of the present study indicate that the exogenous application of STIK and GA_3 has a profound effect on breaking the dormancy of the lenticels up to variable degrees, depending upon their concentrations. A striking increase in the cambial activity on the application of hormones has been demonstrated in several plants (PHILIPSON et al., 1971). The previous reports in the literature do not show an identical situation in respect to the various concentrations of GA_3 except in a few cases. This indicates that the different species have their specific response for each hormonal concentration (GHOUSE and YUNUS, 1974; AHMAD and MATHEW, 1979; BADOLA et al., 1983).

GHOUSE and YUNUS (1974) concluded that both IAA and GA_3 had a profound effect on the lenticel meristem comparable to the vascular cambium in which GA_3 activated maximum number of lenticels when supplied at 0.5 $mgml^{-1}$ level. AHMAD and YUNUS (1979) also observed higher effectiveness of GA_3 than IAA in stimulating the maximum number of lenticels. In a preliminary experiment, ARZEE et al. (1968) reported that GA_3 and naphthalene acetic acid retard the periderm development and lenticel proliferation in Robinia pseudoacacia, which is in contrast to the present findings. Here STIK showed a more pronounced response in inducing the number of lenticels at 1.0 $mgml^{-1}$ level, whereas the area increment has been influenced markedly by GA_3 0.5 $mgml^{-1}$. The area of dormant lenticels of Cedrella toona also got augmented by GA_3 0.5 $mgml^{-1}$ concentration as recorded in our earlier study (BADOLA et al., 1983).

The auxin is the principal limiting factor inducing the cambial activity (HEJNOWICZ and TOMASZEWSKI, 1969) and ultimately also that of the phellogen. Similarly, the promotion of IAA transport in the presence of GA_3 has been recorded earlier in the pea stems by JACOBS and CASE (1965). In the present experiment, the lower concentrations of GA_3 have shown higher effectiveness in inducing the new lenticels. Perhaps these initiated the divisions in the substomatal parenchymatous cells of the periderm which established the formation of lenticel phallogen meristem, confirming the findings of BHAUMIK et al. (1975) who have also observed accelerated formation of parenchymatous cells in the bark with increasing concentrations of GA_3. Besides, the concentrations tested by them were also almost similar to the lower concentrations of the present experiment. In C. toona the highest number of dormant lenticels was activated by GA_3 0.1 $mgml^{-1}$ level of supply (BADOLA et al., 1983).

In conclusion, it can be stated that the dormant lenticels of both the tree species viz. H. integrifolia and P. pashia had a more or less identical response to the various concentrations of STIK and GA_3. More studies of the influence of STIK on different organs of plants including lenticel meristems are required since it is still untested from several points of views. Further investigations, covering additional growth regulators and more species are in progress in this laboratory and will be reported elsewhere.

Acknowledgement

The award of a Research Associat by CSIR, New Delhi, India to the first author (HKB) is gratefully acknowledged.

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Acta Botanica Hungarica 35(1-4), pp. 261-272 (1989)

TRAPPING TEST OF PHENOLIC SUBSTANCES BY CROSS-LINKED INSOLUBLE POLYMERS, AN INTRODUCTION TO OBTAIN UNSTABLE QUINOIDCHALCONE PIGMENTS FROM AN AQUEOUS EXTRACT OF DYER'S SAFFRON FLOWERS

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(Received: 15 January, 1988)

Test for trapping of nine phenolic substances by fifteen cross-linked insoluble polymers were carried out in a neutral buffer system. Among the polymers tested at 6.3 mg/ml in solutions containing phenols, end-group substituted cellulose derivatives were found to be most efficient. Toyo Pearl gels came next. Cellulofines followed this, while Sephadex gels showed far less affinitied for phenols examined. Carthamin was taken up most effectively by the polymers tested. Safflor yellow B, pyrocatechol, caffeic acid, chlorogenic acid, precarthamin, safflor yellow A, and catechol followed this, while only little or no L-3,4-dihydroxyphenylalanine (DOPA) was fixed with the fed polymers. Practical applicability of the phenol trapping technique was tested in an aqueous extract from matured florets of C. tinctorius L.

Keywords: Carthamus tinctorius - trapping test - quinoidchalcone pigment - insoluble polymer

Introduction

Plant phenols including red or yellow phenolic pigments have usually been extracted from the starting materials by using organic solvents. However, especially in case of the constituents are originally unstable, resulting extracts are eventually modified in their chemical characteristics, e.g. the glycosidic forms, the substitute positions, and/or hydroxyl patterns on the molecular structures.

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Abbreviations: DOPA, L-3,4-dihydroxyphenylalanine; AE, aminoethyl; DEAE, diethyl aminoethyl; TEAE, triethyl aminoethyl, QAE, diethyl-(2-hydroxypropyl)-aminoethyl.

Seven Carthamus pigments, kaempferol glycoside (MURTI et al., 1962), luteolin-7-O-glucoside (NAKAOKI and MORITA, 1960), safflor yellow A (TAKAHASHI et al., 1983), safflor yellow B (TAKAHASHI et al., 1984a), safflomin A (ONODERA et al., 1981), precarthamin (TAKAHASHI et al., 1984b), and carthamin (OBARA and ONODERA, 1979; TAKAHASHI et al., 1983) have already been isolated from the leaves or florets of the flowering plant. The former two have 2-phenylchromone ring which is relatively stable in aqueous solutions. While the later five are all consisted of monomeric or dimeric phenyl styryl ketone nuclei with carbon-carbon glucosidic linkages in the structures. They are sensitive to varied pH ranges, drastic solvents, temperatures, and so on. Results from chromatographic analyses suggest that further unknown phenolics are contained in alcoholic extracts from bright yellow saffron florets. For characterizing these components chemically, we are now working to isolate them under the conditions as mild as possible.

The present work is a part of this study, and reports on preliminary tests for trapping the phenolic substances by cross-linked insoluble polymers including newly appeared multipurpose type column packings, cellulofines and Toyo Pearls.

Materials and Methods

Chemicals

End-group substituted celluloses (AE-, TEAE-, and QAE-cellulose) and cellulofines (GCL-25m, GCL-90sf, and DEAE A-800) were supplied from Seikagaku Kogyo Co., Ltd. (Tokyo, Japan). Sephadex gels (G-15, G-25, G-100, LH-20, and DEAE A-50) were purchased from Pharmacia Fine Chemicals (Uppsala, Sweden). Toyo Pearl gels (HW-40f, HW-50f, HW-55sf, and HW-65sf) were obtained from Toyo Soda Co., Ltd. (Tokyo, Japan). Phenols used throughout this study were from our laboratory collections.

Plant material

Seeds of dyer's saffron were shown on a local field in April, 1987. After growing about three months, florets were picked collecting from the matured flowers and immediately frozen at -20 ^{o}C in a freezer before use.

Uniforming and mobilizing of insoluble polymers

Ion exchangers were immersed in deionized and distilled water (2-4 mg/g polymer), stirred for several minutes and resulted fine floating matters were decanted off. The washed exchangers were left to stand over-night at room temperature and swollen in deionized and distilled water. Then they were transferred to appropriate volume of 0.2 M NaOH and stirred successive 2-3 h. The activated anion exchange cellulose, DEAE cellulofine A-800, and DEAE

Sephadex A-50 were washed many times till free of traced ions. Cellulofines (GCL-25m and GCL-90sf), Sephadex gels (G-15, G-25, G-100, and LH-20), and Toyo Pearl gels (HW-40f, HW-50f, HW-55sf, and HW-65sf) were washed repeatedly, kept swollen in water at 2-4 ^{o}C and then used for the phenol trapping tests.

Extraction of polyphenols

Picked florets (30 g) were frozen in liquid nitrogen and crushed with a pistle and mortar. The powdered florets were thawed in 10 vol. methanol/50.0 mM citrate-phosphate buffer, pH 7.0 (1:1, by vol.) by stirring mechanically with a magnetic stirrer for 30-40 min in an ice-bath at 3-4 ^{o}C. The suspension was centrifuged in a refrigerate centrifuge for 20 min at 22000 x g and the supernatant was reduced to 0.5 vol. of the original volume under vaccum. An equal volume of methanol was added, any precipitate which formed was centrifuged off and the volume was reduced again to one third.

Tests for trapping of plant phenols

Weighed amount (20-30 mg) of polymers were mixed stirring into 4.0 ml of 50.0 mM citrate-phosphate buffer, pH 7.0, containing test phenols (100 nmol/ml each). Preincubation was done for 10 s at 25 ^{o}C and the mixture passed through filters, then the filtrate was immediately subjected to the spectrophotometric examination. Absorption change in the solutions was measured within 80-100 s after initiation of the preincubation. The data from the spectrophotometric assays were consulted with standard curves and phenol contents were determined separately. The phenol trapping capacity was defined as the amount of phenolics that taken up by the polymers per min under the standard assay condition and the specific capacity as the trapping capacity per mg insoluble polymer.

Release of trapped phenolics

In this study QAE-cellulose which adsorbed carthamin or safflor yellow B sample was used as a model trapper for the phenol recovery test. An aliquot amount (100 mg wet weight) of the coloured cellulose anion exchanger was separately packed in small glass funnels (1.5x3.2 cm or 1.2x3.0 cm) and eluted with several equivalent volumes of diluted ammonia, guanidine hydrochloride, methylamine hydrochloride, or hydroxylamine hydrochloride. The resulted eluates were adjusted immediately at pH 3.0 by adding glacial acetic acid and used for spectrophotometric determination. The contents of the phenolics in the eluates were calculated from calibration curves.

Tests for trapping of endogenous phenols from an aqueous extract of dyer's saffron florets

An aliquot of the condensed floret extract was loaded on top of QAE-cellulose column (1.0x20 cm, bed vol. 12.4 ml; 1.0 ml) or Toyo Pearl HW-40f column (0.8x23 cm, bed vol. 5.6 ml; 2.2 ml) and developed with deionized and distilled water by gravity flow. The transit liquor was assayed in a spectrophotometer (Shimadzu, type UV 150-02) and changes in contents of the saffron phenolics were estimated by recording UV-VIS light absorption spectra from 200 to 500 nm in 85% methanol. The absorption maxima of printed curvatures on recording papers were collated with those of the data reported previously (FUKUSHIMA et al., 1987).

Partial purification of endogenous safflor yellow B

Orange-yellow QAE-cellulose was eluted with an aliquot of 0.2 M ammonia and the eluate was adjusted to pH 3.5-4.0 by glacial acetic acid. The acidic eluate was treated suc-

cessive four times with one-third vol. of n-butanol, at each extraction fresh n-butanol was added anew. The pooled extracts were condensed under reduced pressure. Dark yellowish brown concentrate was then chromatographed on cellulose columns using n-butanol/acetic acid/water (3:1:1, by vol. and 4:1:2, by vol.) or n-butanol/ethylacetate/methanol/water (4:4:1:2, by vol.) as the developing solvents. Safflor yellow B fraction thus obtained was purified further by passing through Sephadex LH-20 and Toyo Pearl HW-45f gels in distilled water and 65% methanol, respectively.

Measurement of moisture contents in insoluble polymers

Weighed damp polymers (100 mg each) were dried in a Mitamura circulation oven, type 1037 at 80 °C until their weights reach to a stational level. Before checking each dried weight, the polymer was stocked in a desiccator over silica gel for at least 1 h. Measurements were carried out at 25 °C in an air conditioned room and the moisture contents in the test polymers were obtained as average values from each three separate determinations.

Results

Trapping of phenols by anion exchange celluloses

Observation on trapping capacity of nine phenolic substances were severally compared by using three different cellulose anion exchangers. The averaged data from six separate replications are summarized in Table 1. Specific trapping capacities among three anion exchange celluloses are QAE-cellulose (46.1), TEAE-cellulose (33.0), and AE-cellulose (20.9%), whose values correspond to following ratios; 2.2 : 1.6 : 1.0, respectively. Carthamin is shown to be trapped most prominently by all exchangers examined. Safflor yellow A, caffeic acid, chlorogenic acid, safflor yellow B, precarthamin, pyrocatechol, and catechol have less affinity for these cellulose derivatives. DOPA is taken up by the polymers at far lesser level. Averaged value of each phenol trapped was (nmol phenol/mg cellulose derivative/min): carthamin (12.9), safflor yellow A (4.0), caffeic acid (3.8), chlorogenic acid (3.4), safflor yellow B (3.3), precarthamin (3.1), pyrocatechol (2.4), catechol (0.5), and DOPA (0.04).

Trapping of phenols by cellulofines

Three different spheroidal celluloses, which have recently been appeared with commercial name, cellulofine, were used in this study. Test phenols were absorbed by these polymers considerably, though their trapping capacities are not so high as cellulose derivatives (Table 2), which are showsn by the lower ratio of the total phenol adsorption, 1.8 : 1. The

Table 1

Trapping of phenols by cellulose ion exchangers

Phenol	Specific trapping capacity (nmol phenol/mg cellulose/min)		
	AE	TEAE	QAE
Carthamin	10.72	13.52	14.52
Precarthamin	1.60	3.76	3.84
Safflor yellow A	1.60	2.92	7.40
Safflor yellow B	1.64	2.88	5.40
Chlorogenic acid	2.44	2.76	4.84
Caffeic acid	1.76	3.92	5.56
Catechol	0.68	0.04	0.88
Pyrocatechol	0.40	3.12	3.68
DOPA	0.05	0.04	0.02

Average value from six separate replications.

Table 2

Trapping of phenols by cellulofines

Phenol	Specific trapping capacity (nmol phenol/mg cellulofine/min)		
	GCL-25 m	GCL-90sf	DEAE A-800
Carthamin	6.88	7.52	5.76
Precarthamin	1.76	0.16	2.64
Safflor yellow A	0.64	0.64	0.20
Safflor yellow B	2.40	0.84	3.88
Chlorogenic acid	1.84	1.48	3.04
Caffeic acid	1.84	0.32	4.52
Catechol	1.04	0.20	0.20
Pyrocatechol	2.16	3.80	0.92
DOPA	0.02	0.07	0.03

Average value from six separate replications.

Table 3

Trapping of phenols by Sephadex gels

Phenol	Specific trapping capacity (nmol phenol/mg Sephadex gel/min)				
	G-15	G-25	G-100	LH-20	DEAE A-50
Carthamin	3.40	3.32	0.28	5.02	3.56
Precarthamin	1.24	0.92	0.20	0.96	0.80
Safflor yellow A	0	0.76	0.14	0	0.68
Safflor yellow B	1.32	0.72	0.48	3.76	1.92
Chlorogenic acid	1.88	1.24	0.56	2.08	1.28
Caffeic acid	2.24	1.28	0.04	1.84	0.16
Catechol	0.28	0.56	0.04	1.04	1.36
Pyrocatechol	0.88	0.16	1.92	0.92	3.12
DOPA	0.01	0.04	0.03	0.05	0.04

Average value from six separate replications.

Table 4

Trapping of phenols by Toyo Pearl gels

Phenol	Specific trapping capacity (nmol phenol/mg gel/min)			
	HW-40	HW-50	HW-55	HW-65
Carthamin	8.92	8.60	10.60	8.80
Precarthamin	1.64	1.28	1.24	0.56
Safflor yellow A	0.19	0.16	0.16	0.28
Safflor yellow B	3.64	3.12	2.92	1.36
Chlorogenic acid	2.72	1.20	0.48	0.48
Caffeic acid	1.52	0.88	1.48	1.00
Catechol	0.40	0.40	1.84	1.72
Pyrocatechol	1.24	4.04	2.60	3.40
DOPA	0.02	0.02	0.04	0.02

Average value from six separate replications.

specific capacities of the phenol trapping were compared to be: DEAE A-800 (21.2), GCL-25m (18.6), GCL-90sf (15.0), respectively, in average. Their capacities are found to be also varied according to the phenols tested, namely carthamin (6.7), precarthamin (1.5), safflor yellow A (0.5), safflor yellow B (2.4), chlorogenic acid (2.1), caffeic acid (2.2), catechol (0.5), pyrocatechol (2.3), and DOPA (0.04).

Trapping of phenols by Sephadex gels

Five gels were applied to the experiments. The specific values were reduced further, though some descrepancies are seen among gels used. The average ratio of Sephadex gel to that of ion exchange cellulose was: 1:1.9 (see Table 3). Each specific value of test gel was: G-15 (11.3), G-25 (9.0), G-100 (3.7), and DEAE A-50 (12.9), which correspond to following ratios: 3.1 : 2.6 : 1.0 : 3.5, respectively. Individual phenol fixed with the gels is ordered at following concentration, 3.1 (carthamin), 1.6 (safflor yellow B), 1.4 (chlorogenic acid), 1.4 (pyrocatechol), 1.1 (caffeic acid), 0.8 (precarthamin), 0.7 (catechol), 0.3 (safflor yellow A), and 0.03 (DOPA).

Trapping of phenols by Toyo Pearl gels

Four polymers were submitted for the trapping test. The data are listed in Table 4. Relatively higher value of the trapping capacity is seen in carthamin (9.2), safflor yellow B (2.8), and pyrocatechol (2.8) compared with those cellulofines and Sephadex gels, though other phenols remain low as seen following data, namely precarthamin (1.2), chlorogenic acid (1.2), caffeic acid (1.2), catechol (1.1), safflor yellow A (0.2), and DOPA (0.03). Test gels provided us following different values in phenol trapping capacities, (HW-40) 20.3, (HW-50) 19.7, (HW-55) 21.4, and (HW-65) 17.6.

Trapping of endogenous polyphenolics from an aqueous extract of dyer's saffron flowers

Two trappers were selected for the investigations. The results are illustrated in Fig. 1. Polyphenols in the extract are evidently absorbed by the polymers applied as seen changes in UV-VIS light absorption in the figure before of after addition of the polymers to the condensed extract. Little or no O-diphenol colour reaction could be observed in the effluent from QAE-cellulose, after spraying alcoholic ferric chloride solution on spots of air-dried papers.
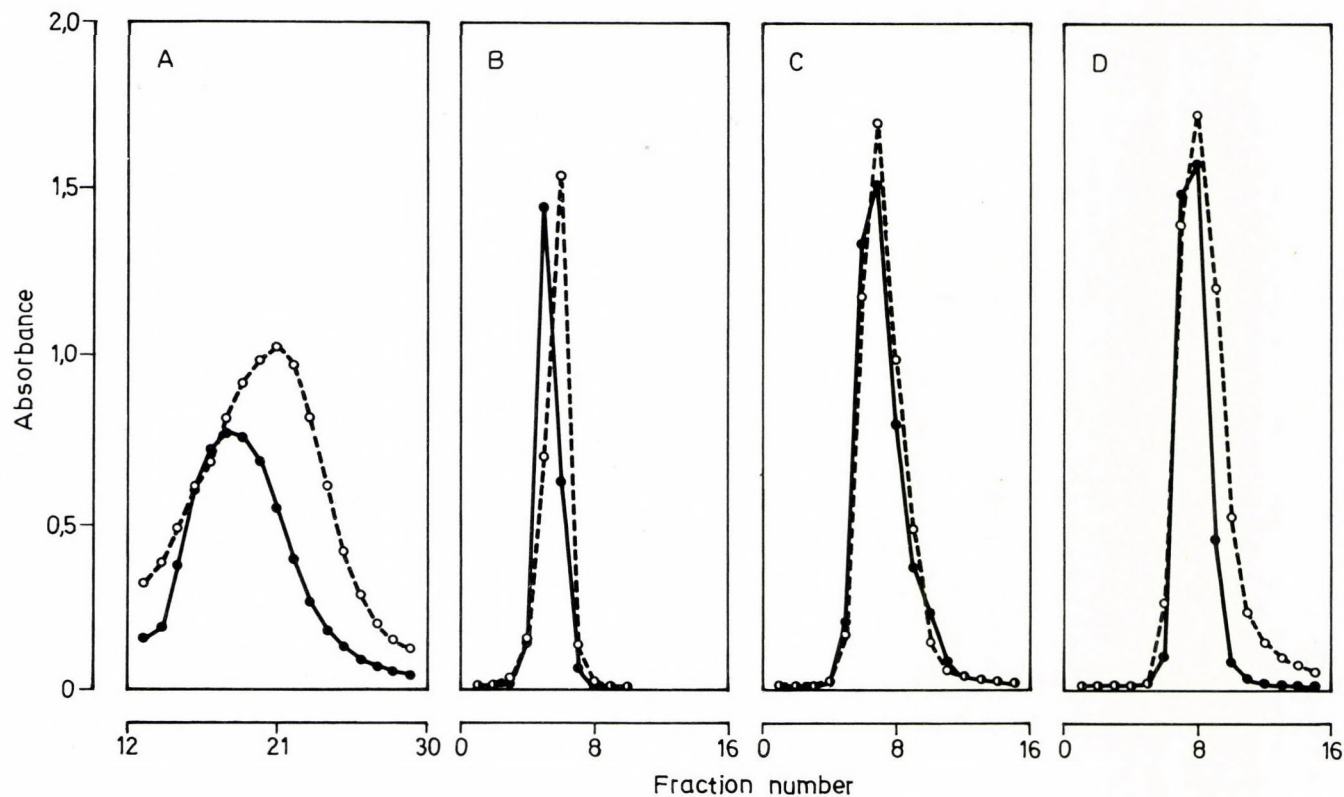
Fig. 1. UV-VIS light absorption spectra of crude extracts from bright yellow florets of dyer's saffron before or after treatment with QAE-cellulose and Toyo Pearl HW-40f. (A) extract before treatment; (B) extract after treatment with QAE-cellulose; (C) extract after treatment with Toyo Pearl HW-40f

Table 5

Release of carthamin and safflor yellow B from coloured QAE-cellulose

Solvent	Concentration (M)	Pigment recovered (%)	
		Carthamin	Safflor yellow B
NH_3	0.02	0	0.90
	0.2	0.95	1.33
	2.0	2.62	2.49
Guanidine-HCl	0.1	0	0.69
	0.5	0	1.66
	1.0	0.08	1.85
Hydroxylamine-HCl	0.1	0	0.70
	0.5	0	0.96
	1.0	0	1.23
Ethylamine-HCl	0.1	0	0.67
	0.5	0	1.36
	1.0	0	1.55

Calibration of endogenous safflor yellow B

To compare the elution profile of trapped safflor yellow B with that of an authentic safflor yellow B, the partially purified sample (1.6 mg) and the authentic specimen (2.0 mg) were applied separately to glass columns of Sephadex LH-20, Toyo Pearl HW-40f, and silica gel C-200, which had been equilibrated previously with desired concentrations of four different developing solvents as indicated in Fig. 2. The fractionation was carried out with the same solvent systems. Both fraction numbers and fraction peaks of the two samples eluted are seen to be coincident well with each other. Identification of the dissociated safflor yellow B sample is in progress.

The released carthamin could not be purified satisfactorily through the processes used here and further works on purification of the pigment was omitted.
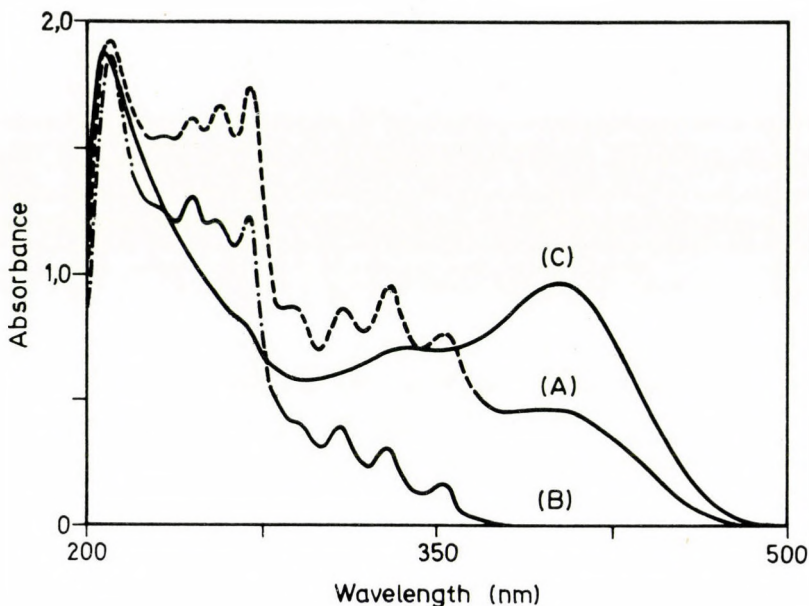
Fig. 2. Comparison of elution profiles of a partially purified floral pigment with an authentic safflor yellow B on calibrated gel columns. (A) Sephadex LH-20 column (1.2 x 31 cm, bed vol. 28.0 ml) eluted with distilled water and each 2.0 ml fraction was collected, (B) Toyo Pearl HW-40f column (1.0 x 18 cm, bed vol. 15.0 ml) eluted with 65% methanol and each 1.0 ml fraction was collected, (C) silica gel column (0.8 x 24 cm, bed vol. 8.4 ml) eluted with iso-propanol/water (7:3, by vol.) and each 0.5 ml fraction was collected, and (D) silica gel column (0.7 x 24 cm, bed vol. 8.1 ml) eluted with n-butanol/acetic acid/water (3:1:1, by vol.) and each 0.5 ml fraction was collected. •——• : partially purified floral pigment; o------o: an authentic safflor yellow B. Experimental data illustrated in each figure were reduced to following ratios (floral pigment; safflor yellow B): one half; one half, one eighth; one twelfth, one fifth; one seventh, one seventh; one sixth. Spectra were taken at 400 nm in 65% methanol

Discussion

Techniques for isolation and purification of plant phenolics have already been well-documented in a vast variety of literatures published (EGGER, 1969; MABRY et al., 1970; HARBORNE, 1975; MARKHAM, 1982; WAGNER et al., 1984). Some of them have also been applied by many investigators for phytochemical examination of secondary metabolites in C. tinctorius. The flowers are known to produce colouring matters, which belong to a member of phenolic constituents. They are very senstivie to drastic acids, bases, and/ or temperatures. Prolonged and oxy-phile treatments in aqueous solutions are also unfavourable to yield high quantities of the pure samples. Therefore,

simple process, speedy operation, and mild conditions always compel us to ensure complete isolation and purification of the phenolic components with novel structures as mentioned above. To overcome these difficulties and to advance phytochemical studies in dyer's saffron further, preparatory tests for finding effective polyphenol trappers seemed to be essential.

The results from the present studies indicate that applied insoluble polymers have varied affinitive capacities for fed phenolic substances including Carthamus pigments. Among these cellulose ion exchangers were most promising. Toyo Pearl came next. Cellulofine followed this, while Sephadex gels were not a level with the former three in the phenol adsorption capacities. Each averaged specific value of the polyphenol trapping ranged as follows: celluloses (3.7), Toyo Pearls (2.2), cellulofines (2.0), Sephadex gels (0.9) and the rate was roughly calculated to be; 43.0 : 25.6 : 23.3 : 8.1%, respectively. The observed affinitive differences are presumably reflected by the chemical and/or physical characteristics of both polymers and phenols in solutions, though these interesting aspects are to be inspected in due course of time. Carthamin had the most strong affinity for all polymers tested. Safflor yellow B, pyrocatechol, caffeic acid, chlorogenic acid, precarthamin, safflor Yellow A, and catechol was also taken up by the polymers but the amounts were far lesser. DOPA was trapped at only little or no level. The average rates were: carthamin (38.9), safflor yellow B (12.2), pyrocatechol (10.7), caffeic acid (10.2), chlorogenic acid (9.7), precarthamin (8.3), safflor yellow A (6.3), catechol (3.4), and DOPA (0.2%). These ratios corresponded to be, 200.0 : 62.7 : 55.0 : 52.4 : 49.9 : 42.7 : 32.4 : 17.5 : 1.0, respectively. In some cases fed phenols were suggested to be adsorbed selectively by the test polymers. This indicates that the phenol trapping technique is applicable to practical isolation and purification of unknown quinoidchalcones in dyer's saffron flowers, provided these polymers are used appropriately. The possibility is supported partially by the data from extraction of endogenous safflor yellow B.

Techniques for separation of phenolics through specific binding with charged or uncharged polymers seem to have been rarely applied if any. At least, as far as we know, no such technique has been reported in any literatures about the isolation and purification of quinoidchacone glycosides from plant extracts. To establish this technique, further studies should be carried out more precisely. Solubilization of trapped compounds under mild conditions, efficient recovery of fixed phenolics, simplifying really the operation process, and so on may be the most important points which

must be examined next. Some of these investigations are now under way in our laboratory and in due course we will report the data elsewhere.

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Acta Botanica Hungarica 35(1-4), pp. 273-277 (1989)

EXTRACELLULAR ADHESIVE SUBSTANCES ON BRYOPHYTE RHIZOIDS

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(Received: 20 January, 1988)

Electron microscopic studies have shown that the attachment of bryophytes to a solid object is accomplished by the rhizoidal production of extra-wall materials in response to contact with the solid object. Histochemistry of the thigmotactically stimulated rhizoids showed the extra-wall materials to be sulphated mucopolysaccharide, a highly viscous, sticky substance which is also involved in the adhesion of microorganisms and algae to solid surfaces.

Keywords: Bryophytes, rhizoids, substratum, adhesion, extra-wall substances, sticky, mucopolysaccharide.

Introduction

The rhizoids of hepatics are, with rare exceptions (e.g. KITAGAWA and KODAMA, 1974) usually non-septate, and are commonly unbranched. Whereas swollen rhizoids, exclusive to hepatic species growing on peat and rotten wood, are always associated with fungal hyphae and may well be absorptive in function (POCOCK and DUCKETT, 1985) rhizoid branching in hepatics and some pleuorcarpous mosses appears to be a response to contact with a solid substratum and this presumably increases their efficiency as organs of attachment (ODU and RICHARDS, 1976).

Little is known about the precise mechanism of adhesion of bryophytes to their substrates. The objective of this paper is to confirm earlier speculations of the presence of extracellular adhesive substances on bryophyte rhizoids.

Materials and Methods

Substrates were prepared by fixing pieces of clean sterilized cover slips and rotten wood (about 6x10 mm) and small chips of rock on molten sterilized Parker medium (KLEKOWSKI, 1969) which was allowed to set.

Cultured shoots of *Lophocolea cuspidata* and selected acrocarpous plus pleurocarpous mosses were aseptically transfered on to media with sterilized substrates such that each shoot

Akadémiai Kiadó, Budapest

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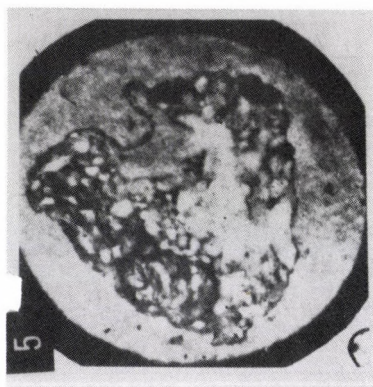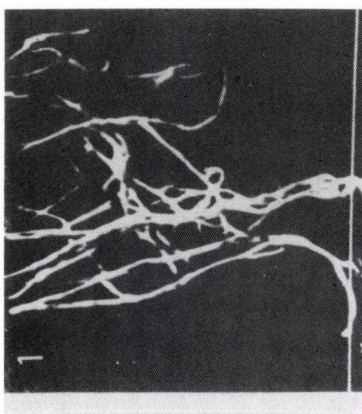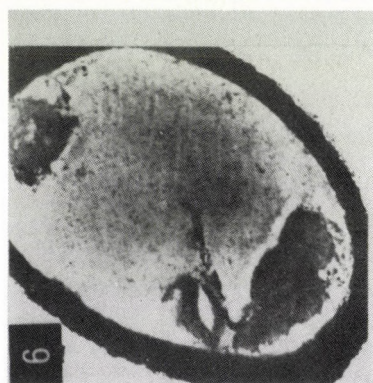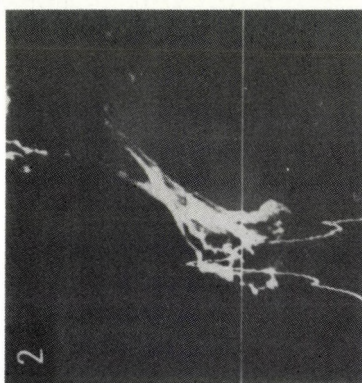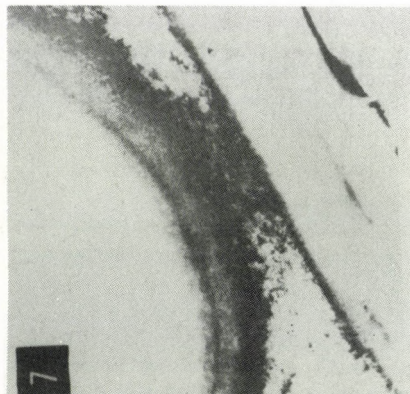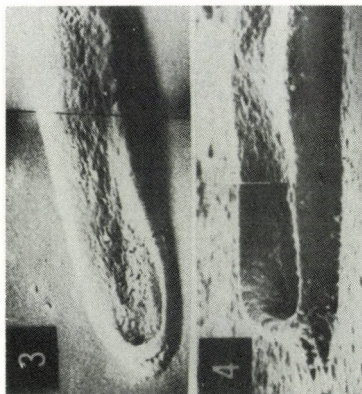
was just touching the wood, rock or cover slip. These were left to grow under continuous fluorescent illumination at a temperature of about 23 °C for 2 weeks after which 8-11 mm shoots with their rhizoids grown over and attached to the substrates were severed and used in further microscopic preparations.

Excised shoots with their rhizoids attached to the pieces of rotten wood were processed for transmission electron microscopy (TEM) while those on glass slips and rock chips were processed for scanning electron microscopy (SEM) and electron probe microanalysis.

Observations

Line scan images for silicon on rhizoids of Lophocolea cuspidata, Hypnum cupressiforme var. cupressiforme and Rhynchostegium riparioides clearly show concentrations of this element specific to the rhizoid tips in contact with the pieces of rock (Fig. 2). In order to discover whether the silicon recorded in this preparation were real features of the rhizoids or contaminations from the rock particles, control rhizoids in contact with smooth glass surfaces and those free from any solid object were treated similarly. Figure 1 shows negative results, demonstrating that the silicon accumulations recorded in Fig. 2 were particles of rock presumably adhering to the rhizoids after contact because of the sticky nature of the rhizoid surfaces.

Examinations of specimens on the SEM were carried out at sixty degrees or more to the vertical to view clearly both the rhizoid tips and the inter-face between rhizoids and subtrates. In all specimens examined distinct thick layers of extra-wall materials were observed at the rhizoid/substrate inter-face (Figs 3-4). Effective attachment of the rhizoids to the substrates by the wall materials was in most cases facilitated by flatening of parts of rhizoids in contact with the substrates. In the pleurocarpous mosses the flattened parts were usually towards the rhizoid tips but rhizoid flattenings extended far behind the apical regions in the acrocarpous mosses.

Plate I

1. Line scan of rhizoids of Hypnum cupressiforme var. cupressiforme after contact with glass (x 160).
2. Secondary electron image with line scans for Si (K α) on rhizoids of Lophocolea cuspidata after contact with rock surfaces (x 160).

3-4. Rhizoids of Rhynchostegium riparioides in contact with glass surface showing thick extra-wall materials at the rhizoid/glass interphase. - 3. (x 1955); - 4. (x 1190).

5-7. Electron micrographs of sections of H. cupressiforme rhizoids. - 5. Free rhizoid (x 13000); - 6. Tip of rhizoid after contact with substratum (x 13000); - 7. Section through the rhizoid/substrate interphase showing fibrillar extra-wall material (x 19000).

The rhizoid cell wall is normally limited on the outside by a thin smooth layer. After rhizoid contact with the substratum intracellular and wall changes apparently result in the tearing away of this thin outermost smooth layer leaving the sticky materials to attach to the substratum (Figs 5-6). The sticky wall materials extend all round the rhizoid cell but are quite distinct at the rhizoid/substrate inter-face (Fig. 7). The advantage of the extra-wall material being all round the cell líes in the ability of the rhizoid to attach to a solid object from any side.

Discussion

The presence of the extra-wall material at the rhizoid/glass or polythene inter-face is demonstrated in the electron micrographs. This substance is insoluble in water since shoots attached to glass did not detach when submerged in water for a long time. The site of observation and formation of the extra-wall material appears to be localised at the tip region in the hepatic and pleurocarpous mosses. These rhizoid tips had been demonstrated to exhibit branching as a thigmotropic response to contact with solid objects (ODU and RICHARDS, 1976). Indications, therefore, are that the sticky wall materials are limited to rhizoid tips in these bryophytes because the apices possess the maximum branching ability.

The cytochemistry of the adhesive materials revealed the presence of complex non-cellulose polysaccharides on the rhizoid walls. The very intense red colour reaction with periodic acid-Schiff reagent (PAS) indicates a non-cellulose polysaccharide (FEDER and O'BRIEN, 1968) while the pinkish colour with toluidine blue indicates the polysaccharide is sulphated (RAWLENCE and TAYLOR, 1972). The secreted extra-wall material thus appears to be a sulphated mucopolysaccharide which shares with gums, slimes and mucilages the characteristics of being highly viscous and very suitable for sticking to solid objects.

Acknowledgement

I would like to thank A. REES and A. DAVIES of the University College of North Wales, Bangor, U.K. for their skillful technical assistance and B.M. SALAMI for preparing the illustrations. Financial support granted by the University of Ife, Ile-Ife, Nigeria is gratefully acknowledged.

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Acta Botanica Hungarica 35(1-4), pp. 279-285 (1989)

CRITICAL NOTES TO CARDAMINE PRATENSIS AGG. IN NE HUNGARY

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Occurrence of a recently described tetraploid species of the Cardamine pratensis agg. in Hungary has been proved by the author. The existence of Cardamine majovskii Marhold and Záborský in Hungary has been confirmed based on karyological studies of Hungarian living populations and morphological studies on Herbarium specimens of Hungarian collections. The species is new for the Hungarian flora.

In connection with the study of the Slovak populations of Cardamine pratensis agg. (for the first results see MARHOLD et ZÁBORSKÝ, 1986; MARHOLD 1984, 1986) the populations of this species complex in North-Eastern Hungary were studied. Presented notes are the result of the karyological and morphological evaluation of the material collected during field trips in the basins of the rivers Bodrog and Tisza in 1985 and 1986. The study of living populations was completed with the study of herbarium specimens in the Hungarian Museum of Natural History (Természettudományi Múzeum) in Budapest (BP[1]).

Chromosome numbers were counted using the method published by MARHOLD et ZÁBORSKÝ (1986). Voucher specimens are deposited in the herbarium of the Institute of Experimental Biology and Ecology of the Centre of Biological and Ecological Sciences of the Slovak Academy of Sciences (SAV); duplicates of herbarium specimens from quoted localities are deposited in the herbarium of the Hungarian museum of Natural History in Budapest (BP).

In the inspected territory populations of Cardamine matthioli as well as recently described C. majovskii Marhold et Záborský, were found.

Cardamine matthioli Moretti in Comolli Fl. Comense 5: 157-159, 1847.
Karyologically studied populations:

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[1] Abbreviations of the herbarium collections are according to Stafleau (ed., 1981).

Akadémiai Kiadó, Budapest

Olaszliszka, to the east of the village, temporary flooded meadows near the dead arm of the Bodrog River, leg. 2. 5. 1985 2n = 16, 18
Erdőbénye, to the east of the village, temporary flooded meadows about 0.5 km from the Bodrog River, leg. 2. 5. 1985 2n = 16
Sárospatak, meadows near the level of the Bodrog River, leg. 3. 5. 1985 2n = 16
Further collecting localities:
Olaszliszka, in the village, leg. 2. 5. 1985
Mezőzombor, near the village, leg. 2. 5. 1985

With the exception of the diploid chromosome number (2n = 16) in one case also the aneuploid chromosome number (2n = 18) was found. A neuploidy has been found only once within Cardamine matthioli, in Moravia (Czechoslovakia) by JAVURKOVÁ in TOMŠOVIC (1986); however, within some other taxa of C. pratensis agg. it is relatively frequent (LÖVKVIST, 1956; URBANSKA-WORYTKIEWICZ et LANDOLT, 1974).

Cardamine matthioli is probably the most frequent species of this complex in the Hungarian territory, which seems to be also the present center of its distribution. Many Hungarian localities of C. matthioli are presented by SOÓ et ISÉPY (1968) as C. pratensis L. subsp. matthioli (Moretti) Arcangeli. SOÓ et ISÉPY (1968) recognize two varieties within C. pratensis L. subsp. matthioli (Moretti) Arcangelli: var. matthioli ("caulis et folia glabra, summum infra puberula") and var. pseudohirta Schur ("tota planta hirsuta"). Such division, however, seems to be unjustified. Most of the individuals of C. matthioli have at least the youngest rosette leaves hairy, the hairs only seldom persist on the older ones. Such variability can be found in almost every population. I haven't found a single completely hairy plant during the study of the herbarium specimens and living populations of C. matthioli. Moreover, C. pratensis L. e. pseudo-hirsuta Schur (sic!) according to the original description (Schur, 1866) probably does not belong to C. matthioli, but rather to C. pratensis L. (s. str.). Neither in the herbarium of the Lvov University in the U.S.S.R. (LW), nor in the Vienna Museum of Natural History, Austria (W), where SCHUR's type herbarium specimens are deposited, is the type specimen of C. pratensis L. e. pseudo-hirsuta Schur present. According to SOÓ et ISÉPY (1968) the variety C. hayneana Welw. var. iliciana Fritsch also belongs to the synonimics of var. pseudohirta. The type specimens of FRITSCH's variety (kept in the herbarium of Vienna University, Austria (WU)), include plants which are either completely glabrous or with only the rosette leaves hairy. None of those specimens correspond to the description "tota planta hirsuta".

Cardamine majovskii Marhold et Háborský Preslia, Praha 58: 194 - 195, 1986

Karyologically studied populations:

Buj, near the village, between the canal Lónyai-cs. and its levee, leg. 21. 4. 1986 2n = 32
Nagytanya (NW of Kótaj), near the village, between the canal Lónyai-cs. and its levee, leg. 22. 4. 1986 2n = 32
Napkor (E of Nyíregyháza), E of the railway station, in the growth of Carex buekii Wimm., leg. 23. 4. 1986 2n = 32
Further collecting locality:
Gergelyiugornya, on the levee of Tisza River, leg. 23. 4. 1986

The only known chromosome number (2n = 32) for this species was confirmed.

During the study of herbarium specimens in the herbarium of the Hungarian Museum of Natural History in Budapest (BP) further specimens of C. majovskii from Hungary were found: Sátoraljaújhely, near Nagy Rozsás Lake, leg. CHYZER, 1879; Sátoraljaújhely, the bank of the Ronyva River, leg. CHYZER, 1879; Tarpa, the wood Téb-erdő, leg. BOROS, 1955. All these herbarium specimens are quoted by SOÓ et ISÉPY (1968: 399) as C. pratensis subsp. pratensis.

The following morphological description of C. majovskii is based on the characters of the Slovakian populations as well as on the population samples from quoted Hungarian localities:[2]

Perennial plant. Rhizome short, simple, rarely branched (when branched, plants are densely caespitous). Stem 15-50 cm tall, glabrous, erect, branched at the base and the upper part, rarely simple. Rosette leaves pinnate 3-27 foliolate, leaflets sessile or indistinctly petiolate, ovate, obovate or oblanceolate, terminal leaflet large, mostly 5-19 mm broad, reniform or cuneate at the base, entire or crenate. The majority of the youngest rosette leaves densely hairy, infrequently sparsely hairy, hairs especially on rhachis invariably adpressed towards the tip of the leaves. Older rosette leaves glabrous, often dying during flowering time. Cauline leaves 3-14, glabrous, pinnatisect (1st and 2nd basal leaves seldom

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[2]The values of the length of sepals and anther filaments given in this description are somewhat higher than those given in articles of MARHOLD et ZÁBORSKÝ (1986) and MARHOLD (1986). The difference arose from the fact that values in quoted articles were measured on dry herbarium specimens, while the present paper is based on measurements of all flower parts of fresh material stuck to adhesive tape (petals measured this way in all cases). The value of 8.0 mm for the length of petals of C. majovskii quoted previously proved to be so rare, that it is not included in the present description.

Fig. 1. Cardamine matthioli Moretti in Comolli
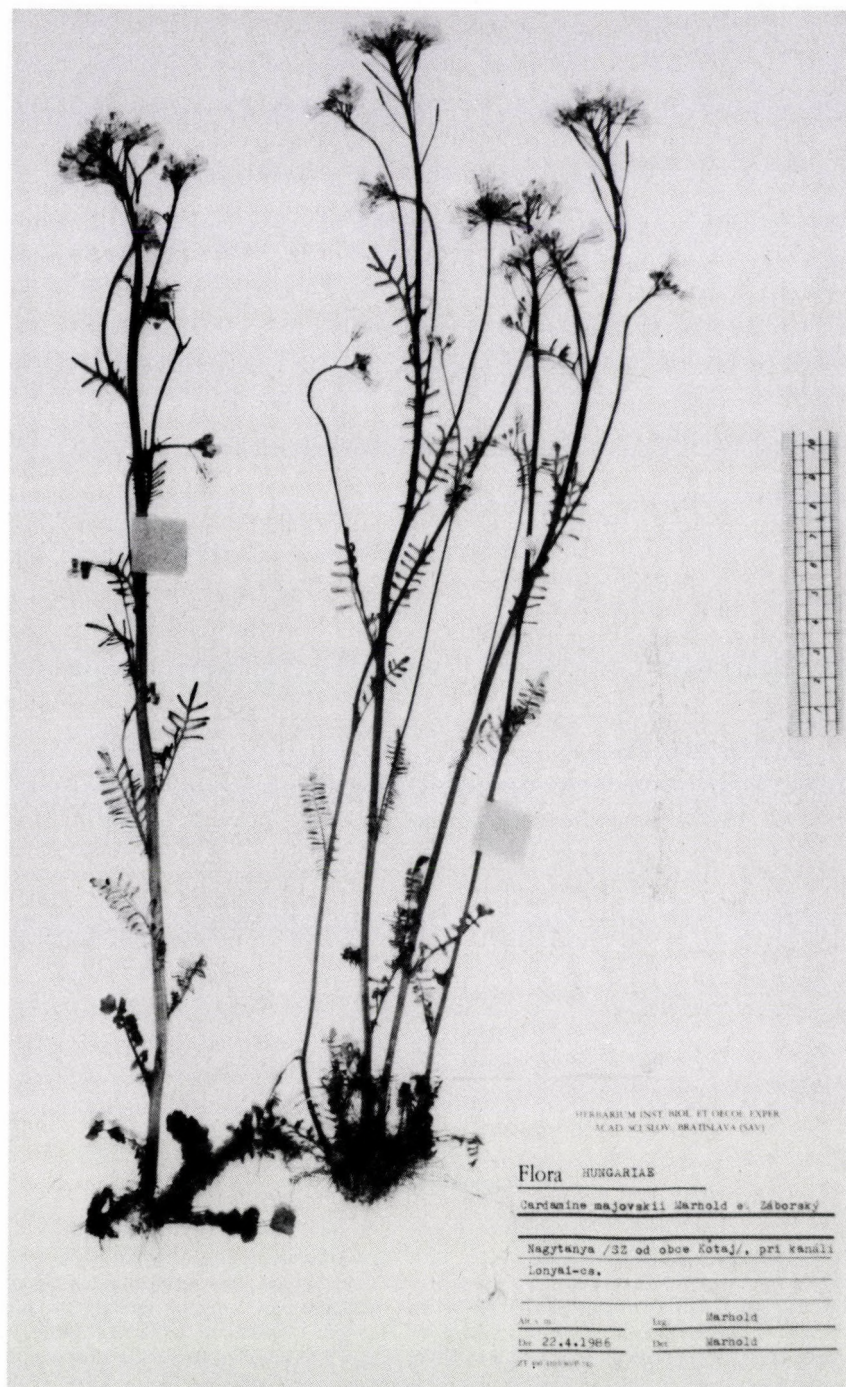
Fig. 2. Cardamine majovskii Marhold et Záborský

pinnate), second lowermost leaf with 9-26 leaflets or sections, third lowermost leaf with 7-25. The number of leaflets or sections diminishes gradually upwards, they are mostly entire, oblanceolate to narrowly lineate (especially at the upper part of stem). Leaflets or sections of middle and lower cauline leaves horizontally spreading, lower leaflets or sections of those leaves often slightly deflexed. Inflorescence racemose, simple or compound. Sepals (3.5 -)4.0 - 5.5 mm long, petals white or with lilac veins, rarely pale lilac, obovate (8.5 -)9.5 - 15.0(- 15.5) mm long, (5.0 -)5.5 - 9.0 (- 10.8) mm broad. Filaments of shorter anthers (2.5 -)3.0 - 5.0(- 5.5) mm long, longer ones (4.5 -)5.5 - 7.5(- 8.0) mm long. Siliques 0.9 - 1.3(- 1.4) mm broad, 18 - 46 mm long, peduncules 9.5 - 24.5 mm long.

Specimens of Cardamine pratensis agg. occurring in Hungary differ from C. majovskii in the following hcaracters:

Cardamine matthioli is similar to C. majovskii in all features, but they differ in the size of flowers. The most suitable differentiating character is the width of petals. Those of C. matthioli are narrower than 5.5 mm, while those of C. majovskii are, as a rule, broader. The average size of pollen grains from several flowers can also serve as a useful differential character being always larger in C. majovskii than in C. matthioli.

Cardamine pratensis L. (s.str.) differs from C. majovskii in having hairs on the rhachis of rosette leaves projecting at right angles and in position of leaflets of all cauline leaves: in C. pratensis spreading under acute angles.

Cardamine dentata Schultes (syn. C. paludosa Kanf, C. palustris Petermann) differs from C. majovskii in having all cauline leaves pinnatifid with leaflets petiolate.

During identification one must always take into consideration several plants from a locality, because almost none of the morphological characters is completely stable.

Acknowledgements

I am deeply indebted to Prof. Dr. A. TERPÓ (Budapest) as well as Mrs. Ágnes BORONKAI (Nyíregyháza) for their care during my stays in Hungary; to Doc. Dr. Harald Riedl (Vienna) for his information about the SCHUR's type herbarium specimens; to the directors of the herbaria of the Hungarian Museum of Natural History in Budapest, Museum of Natural History of the Ukrainian Academy of Sciences in Lvov, and Universities in Lvov and Vienna for the possibility of the Hungarian Museum of Natural History in Budapest, and Universities in Lvov and Vienna for the possibility to study their specimens; to Mrs. Marta HOJOVÁ (Bratislava) for the photographs; finally to Dr. D. J. OSBORN (Prague) for language correction.

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Acta Botanica Hungarica 35(1-4), pp. 287-307 (1989)

EL GÉNERO EXOSTEMA L.C. RICH (RUBIACEAE) EN CUBA*

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(Received: 5 July,1988)

The Antillean taxa of this genus is classified into five sections: sect. Exostema sect. nova, sect. Longiflorae sect. nova, sect. Oligantha sect. nova, sect. Floribundae sect. nova and sect. Polyphyllae sect. nova. For the Cuban taxa a new analytic key followed by short descriptions of the taxa is presented. The new treatment of the Cuban Exostemas contains the descriptions of 9 new species, namely E. cordatum, E. curbeloi, E. glaberrimum, E. lucidum, E. microcarpum, E. monticola, E. pervestitum, E. revolutum, E. scabrum and three new subspecies: E. purpureum ssp. avenium and E. valenzuelae ssp. maestrense and ssp. parvifolium. This interpretation differs from the elaborations of STANDLEY (N. Amer. Flora) and ALAIN (Flora of Cuba) by re-establishing E. eggersii and E. wirghtii on subspecific level, and by merging several species into synonyms. E. obovatum proved to be identical with E. rotundatum Griseb. The great number of the microphyllous species described by different authors from the NE of Oriente are considered here as infraspecific taxa belonging to the variability range of E. myrtifoium Griseb.

Exostema L.C. Richard ex H. et B.-Arbustos o árboles; hojas opuestas, pecioladas o subsésiles; estípulas interpeciolares; flores pequeñas o grandes, axilares y solitarias o en corimbos o panojas terminales, blancas, rojas o amarillas, bracteoladas; tubo del cáliz cilíndrico u obovoide; limbo 5-(-4)-lobulado; tubo de la corola a menudo muy largo, el limbo 5-(-4)-lobulado, los lóbulos oblongos o linear-alargados, filamentos filiformes, alargados; anteras basífijas, lineares, comunmente exertas; disco anular; ovario 2-locular; estilo filiforme, comunmente exerto; estigma acabezuelado, entero o 2-lobulado; óvulos numerosos, ascendentes. Cápsula comunmente oblongo-cilindrica, 2-locular, septicida, 2-valva, las valvas enteras o 2-

*Rubiaceas Cubanas No. 6.

partidas; semillas comunmente numerosas, de testa membranosa, imbricadas, aladas. - Unas 50 especies de Antillas y América tropical.

Las especies antillanas pueden ser clasificadas en cinco secciones siguientes:

Sección Exostema: con inflorescencias terminales corimbosas, multifloras, con flores pequeñas de hasta 2 cm de largo.

Tipo de la sección: Exostema parviflorum L.C. Rich.

Otras especies pertenecientes a esta sección: Exostema cordatum Borhidi et Fernandez, E. curbeloi Borhidi et Fernandez, E. microcarpum Borhidi et Fernandez, E. myrtifolium Griseb. E. pervestitum Borhidi et Fernandez, E. scabrum Borhidi et Fernandez, E. selleanum Urb. et Ekm., E. valenzuelae A. Rich., E. velutinum Standl.

Sección Longiflorae Borhidi con inflorescencias 1-floras, flores largisimas de 15-20 cm de largo.

Tipo de la sección: Exostema longiflorum (Lamb.) Shult.

Otra especies perteneciente a esta sección: E. stenophyllum Britton.

Sección Oligantha Borhidi con inflorescencias uni- a paucifloras, axilares, flores largamente pediceladas, tubo de la corola de 2-5 cm de largo.

Tipo de la sección: Exostema caribaeum (Jacq.) Schult.

Otras especies pertenecientes a esta sección: E. acuminatum Urb., E. glaberrimum Borhidi et Fernandez, E. lancifolium Borhidi et Acuña, E. lucidum Borhidi et Fernandez, E. purpureum Griseb. E. revolutum Borhidi et Fernandez, E. salicifolium Griseb. E. spinosum (Le Vavass.) Krug et Urb.

Sección Floribundae Borhidi con inflorescencias corimbosas terminales, multifloras flores grandes con corolas de 5-10 cm de largo.

Tipo de la sección: Exostema sanctae-luciae (Kent.) Britt.

Otras especies pertenecientes a esta sección: E. angustifolium (Sw.) Schult., E. brachycarpum (Sw.) Schult., E. ellipticum Griseb., E. lineatum (Vahl) Schult., E. monticola Borhidi et Fernandez, E. rotundatum Griseb., E. rupicola Urb., E. subcordatum Krug et Urb., E. triflorum (W. Wright) G. Don.

Sección Polyphyllae Borhidi con inflorescencias terminales, pedunculos 1-floros, hojas a veces ternadas.

Tipo de la sección: Exostema polyphyllum Urb. et Ekm.

Sección monotípica.

Clave analítica para las especies cubanas:

1 a Arbustos o sufrutices de hasta 2 m de altura; hojas lineales a lineal-lanceoladas, flores de 9-15 cm de largo 2

b Arboles o arbustos de mas de 2 m de alto, hojas de otra forma, flores mayormente mas pequeñas 3

2 a Hojas membranosas, estrechadas a agudas en el ápice, ramitas jóvenes pubérulas a vellosas, flores mayormente axilares .....1. E. longiflorum

b Hojas subcoriáceas a coriáceas, obtusas a redondeadas en el ápice, ramitas glabras, flores terminales ....2. E.stenophyllum

3 a Ramitas espinosas, hojas muy pequeñas, de 3-12 mm de largo ....3. E. spinosum

b Plantas inermes, hojas mas grandes 4

4 a Inflorescencias 1-floras, raras veces 2-3-floras, mayormente axilares 5

b Inflorescencias pauci- a multifloras, mayormente terminales 11

5 a Hojas obtusas en el ápice, de 7-11 mm de ancho, sentadas o casi ....4. E. salicifolium

b Hojas agudas o acuminadas en el ápice, pecioladas 6

6 a Hojas membranosas, algo falcadas y mayormente plegadas a lo largo del nervio medio, domaciadas en el envés, flores de 6-10 cm de largo...... .... 5. E. caribaeum

aa Hojas, peciolos y caliz glabros .... var. caribaeum

ab Envés de la hoja pubérula a tomentosa .... var. pubescens ....

b Hojas coriáceas, no plegadas, sin domácias, flores de hasta 3-4 cm de largo 7

7 a Hojas aovadas o elípticas a oblongo-elípticas; el pecíolo corto y recto 8

b Hojas lanceoladas a lineal-lanceoladas o lineal-oblongas, colgantes; pecíolo largo y mayormente flexuoso 10

8 a Margen de las hojas muy revoluto, el ápice obtuso; .... 6. E. revolutum

b Hojas del margen plano o poco recurvo, el ápice mayormente acuminado 9

9 a Hojas elípticas a lanceoladas de 3.5-9 cm de largo, mayormente mates en ambas caras .... 7. E. purpureum

aa Hojas con nervios laterales conspicuos y reticulación aparente, inflorescencias mayormente 3-floras .... ssp. purpureum

ab Nervios laterales y reticulación no conspicuos inflorescencias 1-2-floras .... ssp. avenium

b Hojas aovadas de 2.5-3.5 cm de largo, lustrosas en el haz .... 8. E. glaberrimum

10 a Hojas de 3-7 cm de largo, agudas, muy lustrosas en el haz, el envés glabro .... 9. E. lucidum

b Hojas de 6-9 cm de largo, el ápice obtuso, no lustrosas, pelosas a lo largo del nervio medio del envés, muy coriáceas .....10. E. lancifoium

11 a Flores de mas de 5 cm de largo, hojas de 4-12 cm; estípulas de 3-8 mm, mayormente connadas en un tubo bilobulado 12

b Corola de menos de 2 cm; hojas mayormente de hasta 5 cm de largo, estípulas de 1-3 mm, mayormente libres 14

12 a Hojas obovadas a suborbiculares, tubo del cáliz anguloso, tubo de la corola el doble del largo de los lóbulos ....11. E. rotundatum

b Hojas elípticas o aovadas, mayormente acuminadas o agudas, tubo del cáliz no anguloso 13

13 a Hojas de 5-12 cm; lóbulos del cáliz triangular-subulados, rígidos de 1.5-2 mm de largo, tubo de la corola $\pm$ 2.5 cm de largo de igual largo que los lóbulos ....12. E. ellipticum

b Hojas de 3-6 cm; lóbulos del cáliz lineares, flexuosos de 3-3.5 mm de largo; tubo de la corola de 1.5-2 cm, lóbulos $\pm$ 2 veces mas largos ... .13. E. monticola

14 a Arbustos micrófilos con hojas coriáceas de hasta 3/-4/ cm de largo 15

b Arbustos y árboles con hojas mas grandes 20

15 a Hojas comunmente sin domácias pelosas en las axilas de los nervios del envés 16

b Hojas comunmente con domácias 18

16 a Hojas anchamente acorazonadas de hasta 4 cm de largo, brevemente pubérulas en ambas caras ....14. E. cordatum

b Hojas aovadas o elípticas a suborbiculares, mas pequeñas 17

17 a Hojas de hasta 3.5 cm, pelosas en los nervios del envés; fruto pequeño, subgloboso de hasta 3 mm de largo ....15. E. microcarpum

b Hojas de hasta 2.5 cm; glabras y nítidas en ambas caras, fruto de 6-7 mm .... 16. E. curbeloi

18 a Hojas elípticas a lanceoladas de 2-3.5 cm de largo estrechadas en ambos extremos, fuertemente domaciadas y brevemente pelosas en el envés, nervios laterales 4-5 pares, pecíolo de 2.5-4 cm de largo .... 18. d E. valenzuelae ssp. parvifolium

b Hojas aovadas a suborbiculares o deltoideas de 0.7-1.8 cm de largo, subsésiles, nervios laterales 2-3 pares 19

19 a Hojas escabrosas en el haz con pleos tuberculados en la base ....
.... 17. E. scabrum

b Hojas lisas a plegaditas en el haz sin pelos o tuberculos ....
.... 18. E. myrtifolium

aa Hojas mayormente sin domácias .... a. var myrtifolium

bb Hojas mayormente con domácias .... b. var. barbatum

20 a Hojas densamente aterciopeladas en el envés 21

b Hojas no aterciopeladas a tomentosas en el envés ... 19. E. valenzuelae

ba Hojas aovadas de 5-10 cm de largo, domácias escasas o ausentes, nerviación aparente en el envés .... c. ssp. eggersii

bb Hojas de 3-6 cm, mayormente domáciadas .... bc

bc Hojas elípticas a oblongo-aovadas, atenuadas en la base, membranosas a cartáceas, domácias en las axilas superiores del envés......
.... b. ssp. maestrense

bd Hojas aovadas, obtusas redondeadas a subacorazonadas en la base, subcoriáceas a coriáceas .... be

be Cáliz glabro a glabrescente, hojas obtusas a redondeadas en la base, a veces con pelos largos esparciods en los nervios del envés
.... a. ssp. valenzuelae

bf Cáliz pubérulo a densamente pubescente, hojas redondeadas, truncadas a subacorazonadas en la base, poco abolladas, nervios fuertemente impresos en el haz, corto puberulos en el envés ....
.... e. ssp. wrightii

21 a Hojas lampiñas en el haz .... 19. E. velutinum

b Hojas aterciopeladas en ambas caras .... 20. E. pervestitum

1. Exostema longiflorum (Lamb.) Roem. et Schult. Syst. Veg. 5: 18. 1819.

Basionym.: Cinchona longiflora Lamb. Descr. Cinchona 38. 1797. - "Clavellina de río", "Lirio de río". - Arbusto de 1-2 m, ramas pubérulas o vellositas, cuando jóvenes; estípulas oblongas o lanceoladas, de 2.5-6 mm; pecíolo de 3-12 mm; hojas linear-lanceoladas, estrechamente lanceo-elípticas, u oblanceoladas, de 5-11 por 0.8-2.5 cm, estrechadas en ambos extremos, el ápice agudito, membranosas, albo-pelosas en las axilas de los nervios en el envés, el margen plano; flores axilares y solitarias o 1-3 terminales, pedicelos de hasta 1.5 cm; tubo del cáliz cilíndrico, de 6-8 mm, lóbulos linear-subulados, de 3-6 mm: corola blanca or rosada, tubo de 12-14 cm, los lóbulos lineares, de 4-5 cm; anteras de unos 2 cm; cápsula oval-

elipsoidea, de 1.5 cm, acostillada. - Orillas de arroyos: toda Cuba; Española.

2. Exostema stenophyllum Britt. Bull. Torr. Bot. Club 42: 517. 1915. Tipo: Shafer 3623 Rio Guayabo, Nipe. Arbusto de hasta 2 m, glabro; estípulas de 1-2 mm, obtusas; hojas sentadas, linear-oblanceoladas, de 2-8 cm por 3-10 mm, estrechadas en la base, ± estrechadas hacía el ápice obtuso, coriáceas, el margen subrevoluto; flores terminales, 1-3, pedicelos de 1-1.5 cm; tubo del cáliz de 6-7 mm, oblongo-cilíndrico; lóbulos triangular-subulados, de 2.5-4 mm; corola blanca, el tubo de 9-14 cm, los lóbulos lineares, de 2-4 cm; anteras lineares de 1.8 cm, filamentos del mismo largo; cápsula oblongo-obovoide, de 1.5-2.2 cm, por 8 mm, algo acotillada - Orillas de arroyos: Nipe y Moa., Or.-Endémica.

3. Exostema spinosum (Le Vavass.) Kr. et Urb. in Urban, Ber. Deutsch. Bot. Ges. 15: 262. 1897.
Basionym.: Cinchona spinosa Le Vavass. Obs. Phys. 37: 243. 1790.
Syn.: Catesbaea vavassorii Spreng. Syst. 1: 116. 1825.
Catesbaea elliptica Spreng; DC Prodr. 4: 401. 1830.
Exostema vavassorii Griseb. Cat. Pl. Cub. 126. 1866.
Arbusto de 1-2 m, muy ramoso, ramitas espinosas, pubérulas cuando jóvenes, pecíolo de hasta 1 mm; hojas ovales u oblongas, de 3-12 por 1.5-6 mm, redondeadas a obtusas en la base, redondeadas en el ápice, coriáceas, brillantes en el haz, el margen a menudo sub-revoluto; flores axilares, solitarias, pedicelos delgados, de 5-7 mm; tubo del cáliz oblongo, de 3-4 mm, glabro, lóbulos de 0.5 mm; corola de 1.5-2 cm, lóbulos lineares, de 6-9 mm; estambres 4, exertos, anteras de 4 mm; cápsula oval-oblonga, de 8-12 mm. - Maniguas costeras y sabanas: Or., Cam., LV., Mat., Hab.; Española.

4. Exostema salicifolium Griseb. Cat. Pl. Cub. 125. 1866. Tipo: Wr. 2676.
Arbusto de unos 3 m, glabro; estípulas de 1 mm, deltoideas, agudas; pecíolo de hasta 1.5 mm; hojas oblongo-oblanceoladas o estrechamente elíptico-oblongas, de 2.5 4 cm por 0.7-1.5 cm, agudas o estrechadas en la base, algo estrechadas en el ápice obtuso, subcoriáceas, los nervios laterales poco visibles; flores axilares, solitarias, los pedicelos delgados, de 1-1.8 cm; tubo del cáliz de 3-4 mm, oval-elíptico, lóbulos casi nulos; corola morada por fuera, blanca por dentro, el tubo de 2 cm, los lóbulos lineares, del largo del tubo;

estambres exertos, anteras de 1.4 cm; cápsula elipsoide, de 1.2-1.8 cm. - Maniguas costeras: Hab., PR.- Endémica.

5. Exostema caribaeum (Jacq.) Roem et Schult. Syst. Veg. 5: 19. 1819.
Basionym.: Cinchona caribaea Jacq. Enum. Pl. Carib. 16. 1760.
Syn.: Cinchona jamaicensis Wright Phil. Trans. Roy. Soc. London 67: 506. 1778.
Cinchona myrtifolia Stikes, Bot. Mat. Med. 1: 359. 1812.
Cinchona racemosa Schrank Steud. Nom. Bot. ed. 2. 1: 363. 1840.
Exostema longicuspe Oerts. Vidensk. Meddel. 1852: 48 1852.
"Lirio santana", "Cerillo" "Macagua de rosta". - Arbusto o árbol, a veces de hasta 8 m; estípulas de 2.5-5 mm cilioladas; pecíolo de 3-12 mm; hojas mayormente aovadas a elíptico-oblongas, de 5-11 por 1.3-5 cm, obtusas o agudas en la base, más bien abruptamente acuminadas en el ápice, a veces agudas, membranosas, con grupos de pelos en las axilas de los nervios en el envés, o a veces densamente pelosas, el margen plano; flores axilares, solitarias, los pedicelos de 4-10 mm; tubo del cáliz glabro, de 4-5 mm, lóbulos de 1 mm, anchos, obtusos o agudos; corola blanca, el tubo de 3-5 cm, lóbulos lineares, del largo del tubo; estambres exertos, anteras de 2 cm; cápsula oval o elipsoide, de 1-1.5 cm, oscura, brillante. - Maniguas: toda Cuba e IP.; Fla., Baham., Ant. y Amér. Central.
var. caribaeum con hojas, ramitas y pedicelos glabros
var. pubescens Borhidi et Muñiz Acta Bot. Acad. Sci. Hung. 18: 48, 1973. envés de las hojas peloso a tomentoso, ramitas jóvenes y pedicelo pelosos. - Costa Sur de Baracoa, Española, Mexico.

6. Exostema revolutum Borhidi et Fernandez in Acta Bot. Hung. 35: 301. Arbusto, ramitas 4-angulosas, lampiñas, lustrosas, engrosadas en los nodos, estipulas triangulares, de 1-1.5 mm de largo, pecíolos erguidos, rígidos de 3-5 mm, hojas alargado-elípticaas, 2.5-4.5 por 0.5-1.5 cm, glabras muy coriáceas, el margen muy revoluto. Flores solitarias en las axilas, pedicelos erguidos, rígidos, de 8-12 mm, persistentes, tubo del caliz 3-4 mm de largo, lóbulos 5, lanceolados de 0.7-1 mm, cápsula elipsoide o suborbicular, 10-12 mm por 6-7 mm, lisa. - Matorral serpentinoso seco: Peladeros de Jauco, Gu, - Endémica.

7. Exostema purpureum Griseb. Cat. Plant. Cub. 125. 1866. Tipo: Wr. 2761, Baracoa.

"Vigueta". - Arbusto de hasta 2 m, glabro, ramas gruesas; estípulas de 1-1.5 mm, subcuspidadas; pecíolo de 2.5-7 mm; hojas lanceolado-oblongas, aovado-oblongas, aovadas o elíptico-oblongas, de 3.5-9 por 1.5-4.2 cm, redondeadas a estrachadas en la base, agudas a subacuminadas en el ápice obtuso, coriáceas y brillantes, el margen a menudo revoluto; pedicelos mayormente axilares, solitarios o geminados, muy delgados, de 0.5-2 cm, a veces con pedunculo de hasta 3 mm; tubo del cáliz oblongo-elipsoide, de 4-5 mm, lóbulos pequeños, triangulares, agudos; corola morada por fuera, rosada por dentro, el tubo de 1-1.5 cm; los lóbulos de 1.5 cm; cápsula elipsoide, de 1-1.5 cm, lisa. - Orillas de arroyos: N. de Or.-Endémica.

- ssp. purpureum, con hojas apiculadas en el ápice, el limbo lustroso en el haz, retículo de nervios aparente, inflorescencias mayormente 3-floras. - Gu, Baracoa.

- ssp avenium Borhidi et Fernandez in Acta Bot. Hung. 35: 302. Hojas agudas en al ápice, mates en ambas caras con colores muy diferentes cuando secas, nervios laterales no conspicuos, inflorescencias mayormente 1-/2/-floras. Tipo: Wr. 2680. - Pinares y matorrales serpentinosos, N. de Or.: Ho, SC, Gu. - Endémica.

8. Exostema glaberrimum Borhidi et Fernandez Acta Bot. Hung. 35: 302. - Arbusto de 2-3 m, ramitas rígidas, erguidas, glabras, estípulas alargado-triangulares, de 1.5-2 mm de largo, persistentes, leñosas. Pecíolo de 3-5 mm, erguido, rígido, hojas aovadas, obtusas o redondeadas en la base, acuminada y obtusa en el ápice, 2.5-3.5 por 1.2-1.8 cm, lustrosa en el haz, mates en el envés, coriáceas, glabras, el margen plano. Inflorescencias axilares con 1-2 flores, pedicelos de 5-7 mm, pedunculo de 1-2 mm, tubo del caliz 5-6 mm de largo, lóbulos 5, muy cortos. Corola de 10-12 mm en el tubo, lóbulos de 9-10 mm. - Bosque siempreverde, Yunque de Baracoa. Gu, - Endémica.

9. Exostema lucidum Borhidi et Fernandez in Acta Bot. Hung. 35: 302. - Arbustos o arbolitos, ramitas flexibles colgantes, lustrosas, glabras, ramitas laterales cortas. Estípulas, triangulares de 1-2 mm, persistentes. Pecíolo de 5-12 mm de largo, flexuoso, hojas oblongo-lanceoladas a lineal-lanceoladas de 3-7 por 0.7-1.5 cm, muy brillantes en el haz, glabras en ambas caras, atenuadas en la base, largamente acuminadas y agudas en el ápice, coriáceas, el margen plano. Flores 1-2 en las axilas, pedunculo 2-5 mm, pedicelos de 5-10 mm de

largo, tubo del cáliz de 3 mm, lóbulos 5-6, agudos de 1 mm, tubo de la corola 1.5 cm de largo, lóbulos 5, de igual largo, capsula elíptica de 8-10 mm, lampiña. - Arroyos serpentinosos de Moa, Ho, - Endémica.

10. Exostema lancifolium Borhidi et Acuña in Borhidi et Muñiz, Acta Bot. Hung. 17: 28. 1971. Fig. p. 29.

Ramitas cilíndricas, glabras o pubescentes; estípulas de 1-1.5 mm con un mucrón de igual largo. Hojas colgantes, pecíolo de 7-12 mm de largo, flexible, el limbo lineal-lanceolado, cuneado en la base, largamente acuminado y obtuso en el ápice, 5-8 cm por 0.6-1.1 cm, mate en el envés, subcoriáceo a coriáceo; nervio medio pubescente en el envés, nervios laterales inconspicuous; inflorescencia uniflora, axilar, pedunculo de 3-4 mm, pedicelos de 8-12 mm, glabros. Tubo del cáliz 3-4 mm, pedicelos de 8-12 mm, glabros. Tubo del cáliz 3-4 mm de largo, lóbulos agudos de 0.7-0.8 mm, corola morada, tubo de 0.8-1 cm de largo, lóbulos 4-5, de 0.8-1 cm, cápsula obovada de 1-1.2 cm de largo, glabra. - Matorral de serpentina, Moa, Ho, Gu, - Endémica.

11. Exostema rotundatum Griseb. Pl. Wright. II. Mem. Acad. Amer. N. Ser. 8: 504. 1862. Tipo: Wr. 1258, Monteverde.

Syn.: Exostema obovatum Alain Contr. Ocas. Mus. Hist. Nat. Col. "La Salle" No. 17: 2. 1959.

Arbusto de 6-9 m, glabro; pecíolo de 4-6 mm; hojas ovales o redondeado-ovales, de 5-7.5 por 3.5-4.5 cm, obtusas o agudítas en la base redondeadas a obtusas en el ápice, coriáceas, brillantes en el haz; inflor. terminal corimbosa, paucíflora, los pedicelos de 1-2 cm; tubo del cáliz cilíndrico, de 4 mm, lóbulos triangular-subulados, de 1.5-2 mm, subobtusos; corola pasando de verdoso a blanco y rosado o rojo, el tubo de 4-4.5 cm, lóbulos mitad tan largos; cápsula oblongo-cilindrica, de 1.5-2.4 cm, lisa. - Pinares y bosques: Ho, Gu, Moa - Endémica.

12. Exostema ellipticum Griseb. Pl. Wright. II. Mem. Acad. Amer. N. Ser. 8: 504. 1862. Tipo: Wr. 1257, Monteverde.

Exostema triflorum Wright non G. Don

Exostema floribundum A. Rich. non Roem. et Schult.

Exostema sanctae-luciae Urban non Britten.

"Plateado", "Vigueta", "Lirio santana", "Cinchona". - Arbol glabro, ramas gruesas; estípulas formando vaína, de 2.5-5 mm, caedizas; pecíolo grueso, de 2-8 mm, hojas ovales a elíptico-oblongas, de 5-11 cm,

por 3-4.5 cm, redondeadas a agudítas en ambos extremos, a veces corto-acuminadas, brillantes en el haz, el envés a veces con grupos de pelos en las axilas de los nervios; inflor. terminal, corimbosa, pedicelos de 4-20 mm; tubo del cáliz de 3-3.5 mm, lóbulos triangulares, agudos o acuminados, de hasta 2.5 mm; corola blanca, luego rosada, el tubo de unos 2.5 cm, lóbulos lineares, del largo del tubo; cápsula subcilíndrica, de 1.5-2.8 cm, algo acotillada. - Bosques: Or., Cam., LV., Hab., PR., IP.; Espanola.

13. Exostema monticola Borhidi et Fernandez in Acta Bot. Hung. 35: 000. 1989. -

Arbusto o arbolito, ramitas glabras, estípulas de 5-7 mm de largo, connadas hasta la mitad. Pecíolos de 5-8 mm, hojas, elípticas u oblongo-aovadas de 3-6 por 1.5-3 cm, estrechadas en ambos extremos, cartáceas, glabras en ambas caras, con domácias esparcidas en el envés. Inflorescencia corimbosa terminal 6-8 cm de largo, pedunculo de 2-3 cm, pedicelos de 3-12 mm de largo, tubo del caliz 4-5 mm de largo, lóbulos 5, lineales, flexuosos, de 3-3.5 mm de largo, agudos en el ápice. Tubo de la corola de 1.5-2 cm de largo, los lóbulos ± dos veces mas largos. - Pinares y pluvisilvas montanas, SC, Sierra Maestra, - Endémica.

14. Exostema cordatum Borhidi et Fernandez in Acta Bot. Hung. 35: 000. 1989. -

Arbusto de hasta 2 m, ramitas jóvenes brevemente pelosas, estípulas de 1 mm connadas en un anillo, triangulares, fimbriadas en el margen. Pecíolo de 1-3 mm, hojas acorazonadas a suborbiculares, brevemente apiculadas el el ápice, de 1.2-4 por 1.4-3.6 cm, diminutamente pelosas en ambas caras, domácias ausentes, el margen revoluto, coriáceas. Inflorescencias sésiles, en corimbo terminal, tubo del cáliz 1.5-2 mm de largo peloso a glabrescente, lóbulos 4-5 lineales, 0.7-1 mm de largo, tubo de la corola 7-8 mm, lampino, lóbulos de 2-3 mm. Cápsula subglobosa o anchamente obovada de 3 mm largo y ancho. - Matorral costero en caliza, SC, Santiago de Cuba, - Endémica.

15. Exostema microcarpum Borhidi et Fernandez Acta Bot. Hung. 35: 000. 1989. -

Arbusto de 2-3 mm, ramitas 4-angulosas, pelosas, estípulas traingulares, de 0.5-1 mm, connadas, apiculadas, brevemente denticuladas, en el margen. Pecíolo de 1-4 mm, hojas aovadas de 1.5-3.3 por 1-2.5

redondeada en la base, brevemente apiculada y obtusa en el ápice, el limbo lampiño, peloso en el nervio medio del envés, mayormente sin domácias. Inflorescencia corimbosa, terminal de hasta 2 cm de largo, muy brevemente pelosa, tubo del caliz semigloboso o aovado, de 1-1.3 mm de largo, lóbulos 4-5, triangulares, agudos, de 0.3-0.4 mm, glabros, tubo de la corola de 7-8 mm, lóbulos 2 mm de largo. Cápsula subglobosa o anchamente obovada, 3 mm de largo y ancho arriba. - Matorral costero en caliza, Aguadores, SC. - Endémica.

16. Exostema curbeloi Borhidi et Fernandez in Acta Bot. Hung. 35: 304. 1989. -

Arbusto de 2-3 m, ramitas suberosas, blancas nítidas, esparcidamente pelosas. Estípulas triangulares de 1-2 mm mucronadas en el ápice. Pecíolo de 1-3 mm, hojas anchamente aovadas a elípticas de 1.5-2.5 por 1-2 cm, obtusas or redondeadas en la base, redondeadas o brevemente apiculadas en el ápice obtuso, nitídulas y glabras en ambas caras, coriáceas. Inflorescencia corimbosa, terminal de 2.5 cm de largo, pubescente, bracteas lineal-espatuladas de 3-4 mm, tubo del cáliz de 1 mm de largo, lóbulos 4-5, triangular-lanceolados, 0.5 mm de largo, agudos, tubo de la corola de 5-6 mm, lóbulos de 4 mm. Cápsula oblongo-obovada, aguda en la base, de 6-7 mm de largo .- Orillas de arroyos en bosque littoral, Puerto Padre, Tu, - Endémica.

18. Exostema myrtifolium Griseb. Cat. Pl. Cub. 1866: 125.

Typo: Wr. 2673, en la cercania de Baracoa.

Syn.: Exostema dumosum Alain Contr. Ocas. 1959. 17: 3.
Exostema barbatum Standl. N. Am. Fl. 32. II. 125. 1921.
Exostema crassifolium Standl. N. Am. Fl. 32. II. 124. 1921.
Exostema nipense Urb. Symb. Ant. 9: 521. 1928.
Exostema shaferi Standl. N. Am. Fl. 32: II. 124. 1921.

Arbusto o arbolito de 1-4.5 m, ramitas pelositas, de 1-2 mm, hojas ovales, elípticas, aovadas a suborbiculares, de 1-2.5 por 0.5-1.8 cm, obtusas, redondeadas a subacorazonadas en la base, redondeadas a brevemente apiculadas en el ápice, coriáceas, el margen revoluto, brillantes y glabras en el haz, mayormente con grupos de pelos en las axilas de los nervios del envés. Inflorescencia terminal cimoso-corimbosa pauci- o multiflora, las ramitas pubescentes, o pubérulas. Tubo del cáliz ± 1 mm de largo, lóbulos de 0.5-0.8 blanca, el tubo de 5-7 mm de largo, lóbulos 5 de ± 3 mm, glabros a veces diminutamente pelositos cuando jóven. Cápsula subglobosa a obovada, lisa o

pubérula de 3-5 mm de largo. Bastante variable. Matorrales calizos y serpentinosos en el Norte de Oriente, Ho, Gu, SC, - Endémica.

- var. myrtifolium
- var. barbatum (Standl.) Borhidi et Fernandez comb. et stat. novus

Basionym: Exostema barbatum Standl. Nort. Amer. Fl. 21. II. 125. 1921.

Depués de haber revisado muchos materiales colectados en las distintas zonas calizas y de serpentinitas de todas las montañas del Norte de la antigua provincia Oriente, concluimos, que las caracteristicas dadas para la distinción de las especies mencionadas mezclan tanto en las distintas poblaciones, formando una serie casi innumerable de transiciones, que no permiten mantener estos taxa al nivel de especies.

19. Exostema valenzuelae A. Rich. in Sagra Hist. Nat. Cub. XI. plate 48. 1850. descr. sub nom. E. parviflorum in Sagra Hist. Nat. Cub. X.: 14. 1845. E. parviflorum auct. non E. parviflorum L.C. Rich. in Humb. et Bonpl. Pl. Aequin. 1: 132. 1808. nec. E. elegans Kr. et Urb. in Urb. Symb. Ant. 1: 423. 1899.

Syn.: E. elegans Alain Fl. Cuba 5: 25. 1962. non Kr. et Urb.
E. parviflorum Alain Fl. Cuba 5: 25. 1962. non L.C. Rich.
E. wrightii Kr. et Urb. in Urb. Symb. Ant. 1: 424. 1899.
E. eggersii Urb. Symb. Anat. 9: 521. 1928.
E. parviflorum Standl. N. Amer. Fl. 32: 124. 1921.

Arbusto o arbolito, mayormente de 2-3 m, ramitas pubérulas; estípulas deltoideas, agudas, apiculadas, de 1.5-8 por 0.8-5 cm, obtusas a anchamente redondeadas o acorazonadas en la base, redondeadas a aguditas, a veces algo cuspidadas en el ápice, coriáceas, algo pelosas en las axilas de los nervios en el envés, el margen plano o revoluto; inflor. terminal y axilar, cimosocorimbosa, de 3-6 cm de ancho, densa y multiflora, pedicelos de hasta 2 mm; tubo del cáliz de 2 mm, glabro, lóbulos 4 6 5, triangulares, agudos, de hasta 1 mm; corolablanca, de 7-12 mm, lóbulos 4 6 5, oblongos a aovado-oblongos, de 2 mm; anteras de 1.5-2.5 mm; cápsula oblongo-obovoide a cilíndrica, de 3.5-5.5 mm, lisa. - Maniguas y bosques: Or., LV., PR. - Endémica.

El tipo del Exostema parviflorum L. C. Rich. encontrado en el Museo de Historia Natural de Paris en una planta de Santo Domingo, con lóbulos del caliz lineales, igual o mas largos del tubo y de color rojizo. Es aparentemente conspecífico con el E. elegans de Krug et Urban, que pasa a la sinonimía de la especie nnterior. De esta forma, para las plantas cubanas el nombre de E. valenzuelae A. Rich. es lo que hay que aplicar. Ya Urban en el Symbolae Antillanae 9: 522. 1928. menciona esta posible solución del problema, permitido por el estudio al tipo en Paris, en 1981 por el autor primero (Borhidi 1987). Las poblaciones cubanas tinen lóbulos del caliz triangulares a oblongo-lanceoladas dos o mas veces menores que el largo del tubo del cáliz. Sin embargo, las poblaciones cubanas tienen ciertas variaciones en la forma de las hojas, pubescencia de la inflorescencia, representadas por poblaciones geográficamente delimitadas, que merecen la distición en rango subespecífico.

- ssp. valenzuelae, hojas aovadas, obtusas o redondeadas en la base, nervios laterales hundidos en el envés y con pelos largos esparcidos, domácias presentes, el cáliz glabro o glabrescente. PR. Mat, Ci, SS,
- ssp. maestrense Borhidi et Fernandez in Acta Bot. Hung. 35: 000. 1989.

  Hojas con peciolos de 5-10 mm dd largo, lanceoladas u oblongo-aovadas, 2-3 veces tan largas como anchas, domaciadas arriba de la mitad, glabras. SC, Sierra Maestra
- ssp. eggersii (Urb.) Borhidi comb. et stat. novus.

  Basionym: Exostema eggersii Urb. Symb. Ant. 9: 521. 1928. Hojas de 5-10 cm de largo, mayormente sin domácias, con un reticulación muy aparente en el envés. Gu, Monteverde, Sierra de Imias,
- ssp. wrightii (Kr. et Urb.) Borhidi comb. et stat. novus

  Basionym: Exostema wrightii Kr. et Urb. in Urb. Symb. Ant. 1: 424. 1899.

  Hojas redondeadas, subacorazonadas o truncadas en la base, el limbo ligeramente abollado, nervios laterales hundidos en el haz, pubérulos en el envés, pedicelos y caliz pubérulo a pubescente. Gu, Yunque de Baracoa.

20. Exostema velutinum Standl. N. Amer. Fl. 32. 11. 125. 1921. Tipo: Britton Earl and Wilson 5837, Rio San Juan, Cienfuegos. Arbusto o arbolito de 3-6 m, ramitas densamente pubescentes; estípulas deltoideas, de 1-2 mm, agudas, pubérulas; pecíolos de 3-7 mm, pelositos; hojas aovado-ovales, a rendondo-aovadas, de 3-7 por 1.8-3.5 cm, redondeadas a obtusas o acorazonadas en la base, aguditas a corto-acuminadas en el ápice, el envés densamente aterciopelado, con pelos blancuzcos y con nervios prominentes; inflorescencia terminal, cimoso-corimbosa, de 3.5-7 cm, de ancho; pedicelos de 1-2 mm, pelositos; tubo del cáliz de 1 mm, pelosito, lóbulos 4, triangulares, de 0.5 mm, corola pelosita, tubo de 3-4 mm, lóbulos 4, aovados, de 1 mm; cápsula obovoide, de 3 mm, pelosita. - Manigua costera: LV. - Endémica.

21. Exostema pervestitum Borhidi et Fernandez in Acta Bot. Hung. 35: 307. 1989. Tipo: León 19389, Llano de Maisi. Difiere de la especie anterior en tener hoja densamente aterciopeladas en ambas caras, cáliz y corola dos veces mas grandes, cápsula mas grande, toda la inflorescencia densamente hirsuta. Matorrales costeros, Sur de Baracoa, Gu, - Endémica.

Apéndice

Descriptción de los taxa nuevos

EXOSTEMA L.C. RICH.

Sectio Exostema sectio nova: inflorescentiis terminalibus corymbosis, multifloris, floribus parvis, usque and 2 cm longis.

Typus sectionis: Exostema parviflorum L.C. Rich.

Species alterae huius sectionis: E. cordatum Borhidi et Fernandez, E. curbeloi Borhidi et Fernandez, E. microcarpum Borhidi et Fernandez, E. myrtifolium Griseb., E. pervestitum Borhidi et Fernandez, E. selleanum Urb. et Ekm., E. velutinum Standl. E. scabrum Borhidi et Fernandez, E. valenzuelae A. Rich.

Sectio Longiflorae Borhidi sect. nova: inflorescentiis unifloris, floribus longissimis, 15-20 cm longis plantae suffruticosae.

Typus sectionis: Exostema longiflorum (Lamb.) Schult.

Altera species huius sectionis: E. stenophyllum Britt.

Sectio Oligantha Borhidi sect. nova: Inflorescentiis uni- vel pauci-floris, axillaribus, floribus longe pedicellatis, tubo corollino 2-5 cm longo.

Typus sectionis: Exostema caribaeum (Jacq.) Schult.

Alterae species huius sectionis: E. glaberrimum Borhidi et Fernandez, E. lancifolium Borhidi et Acuña, E. lucidum Borhidi et Fernandez, E. purpureum Griseb., E. revolutum Borhidi et Fernandez, E. salicifolium Griseb. E. spinosum (Le Vavass.) Krug et Urb.

Sectio Floribundae Borhidi sect. nova: inflorescentiis terminalibus corymbosis multifloris, corollis 5-10 cm longis.

Typus sectionis: Exostema sanctae-luciae (Kentish) Britt.

Species alterae huius sectionis: E. angustifolium (Sw.) Schult., E. brachycarpum (Sw.) Schult., E. ellipticum Griseb. E. lineatum (Vahl) Schult., E. monticola Borhidi et Fernandez, E. rotundatum Griseb., E. rupicola Urb., E. subcordatum Krug et Urb., E. triflorum (W. Wright) G. Don.

Sectio Polyphyllae Borhidi sect. nova: inflorescentiis terminalibus, pedunculis unifloris, foliis rariter ternatis.

Typus sectionis: Exostema polyphyllum Urb. et Ekm. Sectio monotipica.

6. Exostema revolutum Borhidi et Fernandez sp. n.

Frutex vel arbor parve. Rami ascendentes, rigidi, hornotini 4-angulati, nitidi, glabri, nodis incrassatis suffulti, veteriores cylindracei, cinerei, longitudinaliter striati, et transversaliter fissurati. Stipulae triangulares, 1-1.5 mm longae, coriaceae, glabrae, plerumque non vel minute mucronatae. Folia 3-5 mm longe petiolata, petiolis ascendentibus rigidisque suffulta, oblongo-elliptica vel leviter oblanceolata, 2.5-4.5 cm longa et 0.5-1.5 cm lata, basi longe attenuata et in petiolum protracta, apice sensim angustata apice ipso obtusiusculo vel obtuso, nervo medio supra valde impresso, subtus carinato-prominenti, sub apice saepe evanescenti, lateralibus utroque latere 3-6, utrinque obsolete prominulis, rariter in axillis minute scrobiculatis, utrinque nitida, glabra et papillis minutissimis punctulata, margine valde revoluta, coriacea.

Flores axillares solitarii. Pedunculus nullus, bracteae inaequales, 0.5-1 mm longae, basi connatae vel 1-2 mm longe distantes, minores triangulares majores ovatae, apice acuminatae, a basi pedicelli 1-2 mm longe obsitae. Pedicelli arcuato ascendentes, rigidi, 8-12 mm longi, fructu caduto persistentes, calycis tubus oblongatus 3-4 mm longus, supra ovario non vel levissime productus sed manifeste ampliatus, lobi 5, 0.7-1 mm longi, lanceolati, distantes. Corolla non visa. Fructus ellipticus vel subordbicularis, 10-12 mm longus et 6-7 mm latus septo leviter productus, calyce coronatus. Placentae e basi loculorum ascendentes, in sectione transversali triangulares, semina verticaliter disposita, orbicularia, 4-5 mm in diametro, circumcirca alata, ala basi bilobulata lobis rotundatis.

Holotypus: HAJB 39753; Cuba Orientalis; prov. Guantánamo; Laderas al noroeste de la confluencia del Rio Baracoa con el arroyo del Cayo, Peladeros de Jauco. - Leg.: BERAZAIN, CAPOTE, CATASUS, DUHARTE, LÓPEZ. 20.2. 1979. Isotypi: HAJB.

Specimina examinata: Baracoa, Peladeros de Jauco, 300-400 m.s.m. Leg. BISSE et KOEHLER HAJB 5610; - Ibidem, BISSE HAJB 17138; - La Tinta; Cuabales de Peladeros de Jauco, Leg.: BISSE, DIAZ, STOHR. 10.2. 1978. HAJB 36745. - Cuchillas de Toa, Cayo Fortuna, a lo largo del Rio Toa. BISSE, HAJB 16918.

7. Exostema purpureum Griseb. Cat. Pl. Cub. 125. 1966.

- ssp. purpureum, foliis apiculatis, supra nitidis, nervis conspicuis reticulatis, inflorescentiis plerumque 3-floris. - Baracoa.
- ssp. avenium Borhidi et Fernandez ssp. nova

A typo differt foliis acutis, utrinque opacis, in sicco valde discoloribus, nervis lateralibus utrinque inconspicuis, inflorescentiis plerumque 1(-2)-floris.

Holotypus: WRIGHT 2680; Cuba Orientalis in HAC. Isotypi: GH, NY, BM, S, UD.

Distributio: Sierras de Nipe, Cristal, Moa y Toa.

8. Exostema glaberrimum Borhidi et Fernandez sp. n.

Frutex 2-3 m alta. Rami rigidi, adscendentes, leviter angulati, glabri. Stipulae oblongo-triangulares, 1.5-2 mm longae, apice saepe mucronatae, patentes, persistentes demum coriaceae vel lignosae. Folia 3-5 mm longe petiolata, petiolis rigidis, erectisque suffulta, oblongo ovata, basi obtusa vel rotundata brevissime in petiolum protracta, antice acuminata, apice ipso obtusiuscula, 2.5-3.5 cm longa et 1.2-1.8 cm lata, sub medio latissima, nervo medio supra impresso, subtus prominulo, lateralibus utroque latere 3-5 usque ad dimidium limbi utrinque prominulis, deinde obsoletis, lamina supra nitida, subtus opaca, utrinque glabra, coriacea, margine plano vel tenuiter recurvo.
Inflorescentiae axiallares 1-2-florae. Pedunculus 1-2 mm longus, pedicelli 5-7 mm longi. Calycis tubus oblongatus, superne ampliatus, 5-6 mm longus, sub lobis 2 mm latus, lobi 5, triangular-subulati, minuti, cca 0.5 mm longi. Corollae tubus 10-12 mm longus, sub lobis 2 mm latus, lobi oblongo-elliptici, 9-10 mm longi et 3 mm lati, margine undulati, tubo purpureo, lobis albis, antherae 5-6 mm longae, exsertae.

Holotypus: HAJB 58878. Cuba Orientalis; Prov. Guantánamo, Baracoa; parte alta del Yunque de Baracoa; bosque siempreverde mesófilo. Leg. ARIAS, DIAZ et al. 17. 04. 1986.

9. Exostema lucidum Borhidi et Fernandez sp. n.

Rami flexuosi, nutantes, nitidi, glabri; hornotini longitudinaliter striati, veteriores suberosi, fissurati, albescentes; ramuli laterales breves, usque ad 4-5 cm longi. Stipulae triangulares, 1-2 mm longae apice mucronibus aequilongis, demum lignosae, persistentes. Folia oblongo-lanceolata vel lineari-lanceolata, petiolis 5-12 mm longis, superne canaliculato-duplicatis suffulta, 3-7 cm longa et 0.7-1.5 cm lata, sub medio latissima, nervo medio supra impresso, subtus leviter prominenti, lateralibus utrinque nullis, limbus supra lucidus, in sicco transversaliter plicatulus, subtus opacior et longitudinaliter lineolatus, basi longe angustatus et in petiolum protractus, antice longe acuminatus et acutus utrinque glaber, margine planus, coriaceus.

Inflorescentiae axillares, 1-2-florae; pedunculus 2-5 mm longus, bracteae lineares usque ad 1 mm longae, pedicelli flexuosi, tenues, 5-10 mm longi. Calycis tubus ellipticus, ± 3 mm longus, sub lobis leviter contractus, lobi calycini 5-6, triangulares, acuti, 1 mm longi; tubus corollae cca. 1.5 cm longus, lobi 5, tubo ± aequilongi, antherae 6-7 mm longae, exsertae, Capsula fructifera elliptica, 8-10 mm longa, glabra.

Holotypus: HAJB 42659; Cuba Oriental; Moa; Barranco del Arroyo Jaragua cerca de Minas Jaragua. Prov. Holguin. Alt.: 300 m.s.m. Leg.: ALVAREZ et al. 3. 05. 1980. Isotypi: HAJB;

Specimina examinata: HAJB 11597. Prov. Oriente: Moa, La Melba, valle del arroyo grande en la falda sur de la Sierra de Moa. Leg.: BISSE y LIPPOLD 28. 12. 1968. - HAJB 56242. Moa; Alrededores de la Mina Mercedita, cabezadas del Rio Jaguani. 19. 04. 1985. Leg.: ALVAREZ et al.

13. Exostema monticola Borhidi et Fernandez sp. n.

Frutex vel arbor parva. Rami hornotini cylindracei, glabri, internodiis 0.5-2 cm longis. Stipulae 5-7 mm longae, supra medium in tubum 3-5 mm longum connatae, apice rotundatae. Folia 5-8 mm longe petiolata, elliptica vel oblongo-ovata, vel oblongo-elliptica, 3-6 cm longa et 1.5-3 cm lata, basi sensim angustata et in petiolum protracta, apice acuta vel breviter acuminata el obtusa, nervo medio supra leviter impresso, subtus prominenti, lateralibus utroque latere 4-5 obsoletis, subtus tenuiter prominulis, in axillis domatiis scrobiculatis vel sparse pilosis, frequenter ausentibus suffulta, supra in sicco nigra et opaca, subtus brunnea, chartacea vel subcoriacea, utrinque glabra, margine plerumque revoluta.

Inflorescentia cymoso-corymbosa, usque ad 6-8 cm longa et 6-12 cm in diametro; pedunculi 2-3 cm longi, bracteae euphylloideae, lanceolatae et petiolatae vel ovatae et sessiles, pedicelli 3-12 mm longi, glabri. Calycis tubus obovatus vel oblongus, cylindraceus, 4-5 mm longus; lobi 5 lineares, subulati, flexuosi, 3-3.5 mm longi, apice acuti. Corollae tubus 1.5-2 cm longus, lobi 2.5-3 cm longi, 1-2 mm lati, tubum quasi duplo superantes. Antherae 8 mm longae, stylus 5 cm longus, stigma globosum. Fructus non visus.

Holotypus: L.F. 2314 HAC; Prov. Oriente; Sierra Maestra, Loma Pino del Agua, Alto de Valenzuela 1200-1400 m. Leg. LOPEZ FIGUEIRAS, 11. 08. 1955. Isotypus: HAC, HAJB.

Specimina examinata: LEÓN 10982 HAC; Cuba orientalis; Sierra Maestra, jul. 1922.

A specie proxima (Exostema rotundatum Griseb.) foliis minoribus, margine revolutis, nervis lateralibus obsoletis, lobis calycinis linearibus et longioribus, lobis corollinis tubum ± duplo superantibus differt.

14. Exostema cordatum Borhidi et Fernandez sp. n.

Frutex usque ad 2 m alta. Rami cylindracei, albescentes, longitudinaliter striati, lenticellis elongatis sparse obsiti. Ramuli hornotini breviter hirsuti. Stipulae in annulum 1 mm latum connati, ipsae triangulares, margine breviter fimbriatae, apice mucronatae. Folia 1-3 mm longe petiolata, cordiformia, suborbicularia vel rariter late ovata, basi cordata vel rotundata, antice brevissime apiculata, obtusiuscula vel acuta, 1.2-4 cm longa et 1.4-3.6 cm lata, nervo medio supra impresso, subtus prominenti, lateralibus utroque latere 3-4 sub angulo 80-90° abeuntibus, arcuatis et utrinque ante marginem conjunctis, limbo pilis suavibus brevissimis utrinque pubescenti, domatiae absentes, margine revoluto, coriaceo.

Inflorescentiae sessiles corymbosae, puberulae vel glabrescentes, usque ad 2-3 cm longae et 5 cm in diametro. Tubus calycinus ovatus, 1.5-2 mm longus, puberulus vel glabrescens lobi 4-5, lineares, inaequales, 0.7-1 mm longi, dimidio tubi aequilongi. Corollae tubus 7-8 mm longus, glaber, lobi 2-3 mm longi, antherae 3-3.5 mm longae. Fructus subglobosus vel late obovatus, 3 mm longus et latus. Semina 1 mm longa, oblongo triangulata, bialata, basi unilateraliter breviterque caudata.

Holotypus: 6331[a] Sra HERMELIA CASAS (HAC); Cuba, prov. Oriente, Sardinero, en un paredón. Dec. 1948. - Isotypus: 6331[b] Hno CLEMENTE (HAC).

Specimina examinata: El Sardinero, L.F. 317 - Sardinero, CLEMENTE et CRYSÓGONE 5903; Subida al Morro, CLEMENTE 3167. San Antonio del Sur, Abra Mariana, 5 km al NE, ALVAREZ et al. HAJB 43069.

15. Exostema microcarpum Borhidi et Fernandez sp. n.

Frutex 2-3 m altus. Rami cylindracei, grisei, longitudinaliter striati. Ramuli tenuiter 4-angulati, brevissime patenter pilosi. Stipulae in annulum 0.5-1 mm latum connatae, ipsae deltoideo-triangulares, margine membranosae et brevissime denticulatae, apice mucronatae, dorso pilosae. Folia 1-4 mm longe petiolata, ovata, 1.5-3.3 cm longa, 1-2.5 cm lata, basi rotundata vel subcordata, antice breviter apiculata, apice ipso obtuso, margine revoluta; nervo medio supra impresso, subtus bene prominenti, lateralibus utroque latere 3-4 supra tenuiter impressis vel obsoletis, subtus prominulis, ante marginem conjunctis, in sicco rufo-brunneis, cum nervo medio brevissime pilosis, domatiis plreumque absentibus, cetera glabra, chartacea vel coriacea.
Inflorescentiae sessiles, corymbosae, usque ad 2 cm longae et 3-4 cm in diametro, brevissime pilosae. Bracteolae lineares, flexuosae, 0.5-1 mm longae. Calyx semiglobosus vel ovatus, tubus 1-1.3 mm longus, lobi 4-5, triangulares, acuti, 0.3-0.4 mm longi, glabri. Tubus corollae 7-8 mm longus, superne sensim ampliatus, lobi 2 mm longi, antherae 2 mm longae. Fructus subglobosus, vel late obovatus 3 mm longus et superne 3 mm latus. Semina elliptica, 1 mm longa, bialata, ecaudata.

Holotypus: L.F. 718. HAC; Cuba; prov. Oriente; Santiago de Cuba; Cerca de la desembocadura del Rio San Juan, Playa de Aguadores. Leg.: M. LOPEZ FIGUEIRAS 26. 10. 1952. Isotypus: HAC, HAJB, NY.

Specimina examinata: Aguadores, CLEMENTE 2119, Nov. 1936. Aguadores, G.B. BUCHER 313; - Howard 5826. NY., Britton 1860, NY, - El Morro, Santiago de Cuba, CLEMENTE 2217, 18. 11. 1939., Clemente, 5903, Sardinero, 1948.

16. Exostema curbeloi Borhidi et Fernandez sp. n.

Frutex parvus, 2-3 m altus. Rami suberosi, albescentes, nitidi, ramuli hornotini in sicco nigri, striati, sparse puberuli. Stipulae brunneae, triangulares, apice mucronatae, 1-2 mm longae. Folia 1-3 mm longe petiolata, late ovata, rariter elliptica, 1.5-2.5 cm longa et 1-2 cm lata, basi obtusa vel rotundata, apice ipso obtuso; nervo medio supra impresso, subtus prominenti, lateralibus utroque latere 3-4 supra obsoletis, subtus prominulis et tenuissime anastomosantibus, limbo in sicco supra nigricanti, subtus flavo-brunneo, utrinque nitenti et essentialiter glabro, coriaceo.
Inflorescentiae sessiles, cymosae, puberulae, usque ad 2.5 cm longae et 3-4 cm in diametro. Bracteae lineari-spathulatae, 3-4 mm longae, bracteolae lineares, flexuosae et 1 mm longae. Calycis tubus 1 mm longus, glaber, lobi 4-5, triangulari-lanceolati, 0.5 mm longi, acuti, tubo duplo breviores. Corollae tubus 5-6 mm longus, glaber, lobi 4 mm longi. Fructus oblongo-obovatus, 6-7 mm longus, basi longe attenuatus. Locula 2, semina 2 per locula, triangularia, bialata, 1.5-2 mm longa, basi asymmetrice caudata.

Holotypus: Herb. ROIG 5857 in HAC; Cuba, prov. Oriente, Puerto Padre, orillas de arroyos. Leg.: CURBELO 105; 8. 12. 1931. - Isotypus: HAC.

17. Exostema scabrum Borhidi et Fernandez sp. n.

Frutex ramosus, usque ad 2 m altus. Rami hornotini obscure 4-anguli, longitrorse striati, dense puberuli, veteriores cylindracei, grisei, glabri. Stipulae interpetiolares triangulares usque ad 0.5 mm longae, margine membranaceae et fimbriatae, dorso puberulae. Folia late ovata vel suborbicularia, sessilia vel subsessilia, petiolis usque ad 1 mm longis suffulta, 7-14 mm longa et 6-13 mm lata, basi cordata, apice rotundata, nervo

medio supra valde impresso, subtus prominenti, lateralibus utroque latere 2-3, supra crassiuscule impressis, subtus prominulis, lamina supra nitida, pilis basi valde incrassatis densissime dispositis scabra, subtus opaca et pilis brevibus suavibusque pubescens et in axillis nervorum lateralium domatiata, margine valde revoluta, bullata et rigide coriacea.
Inflorescentia corymbosa, terminalis sessilis, multiflora, 1.5 cm longa et 3 cm lata. Bracteae lineares, 1-2 mm longae. Rami inflorescentiae 6-8 mm longae, breviter et patenter hirsutae, pedicellis 2-3 mm longis, hirsutis. Calycis tubus obovatus, 1.5-2 mm longus, adpresse pilosus, lobi 5, lineares, 1-1.5 mm longi, apice obtusi, tubo quasi aequilongi. Capsula septicida, obovata, 3-4 mm longa, basi acuta, ferrugineo-puberula. Cetera ignota.

Holotypus: HAJB 48177. Cuba, Prov. Guantanamo, San Antonio del Sur, Abra Mariana, monte seco, suelo calizo, 100-300 m. alt. Leg.: BISSE et al. 21. 05. 1982.

19. Exostema valenzuelae A. Rich. in Sagra Hist. Nat. Cuba XI. plate 48. 1850.

- ssp. valenzuelae, foliis ovatis basi obtusis vel rotundatis, subtus ad nervos saepe sparse longeque pilosis, domatiatis, calyce glabro vel glabrescenti.

Specimina examinata: WRIGHT 1260; Cuba Occidentalis, Pinar del Rio; Santa Cruz de Pinos, 3. 10. 1862. - SHAFER 13480; Sumidero limestone hills, 2-4. 08. 1912. - LEÓN 3205; - Loma de Cajalbana: ALAIN 1372, ALAIN 1458, MATIAS YERO 1299, ACUÑA 15844, BISSE et al. HAJB 32683; - Loma Pelada o Peluda o Preluda al Oeste de Cajalbana: ACUÑA 16602, M. FERNANDEZ et al. HAC 29190, BISSE et al. HAJB 32603; _ Sierra del Ancón, Viñales, ALAIN 6852; - Cuabales al Este de Cajalbana, ALAIN 1667; - Subida al Pan de Guajaibón, ALAIN 6772; - Sierra de la Güira, Mogote del Faustino, BORHIDI et CAPOTE BP; - Sierra del Rosario, Paredones calizos del Rangel, ALAIN 1265, Las Villas: Manantiales Cienfuegos, Sierra de Escambray, P. HERRERA et al. HAC. 35176.

- ssp. maestrense Borhidi et Fernandez ssp. nova

Arbor parva, usque ad 6-8 m alta. Rami cylindracei, glabri, ramuli hornotini adpresse minuteque puberuli. Stipulae late triangulares, acutae, cca 1 mm longae, apice 0.2-0.3 mm longe mucronatae. Folia 5-10 mm longe petiolata, lanceolata vel ovata, basi attenuata, obtusa vel rotundata, apice acuminata, obtusiuscula vel acuta, 3.5-6 cm longa et 1.8-3.6 cm lata, 2-3-plo longiora quam latiora, medio vel sub medio latissima, chartacea vel membranosa; nervo medio supra leviter impresso, lateralibus utroque latere 4-6 sub angulo 50-60^{0} abeuntibus, supra tenuiter impressis et anastomosanti-reticulatis, subtus tenuiter prominulis et impresse reticulato anastomosantibus, supra nitentia, subtus pallidiora et in angulis adapicalibus (supra medium) laminae nervorum mediorum domatiata, glabra. Inflorescentiae terminales 1.5-3 cm longe pedunculatae, usque ad 4.5 cm longae et ad 6 cm de diametro, corymbosae, adpresse puberulae. Bracteae euphylloideae 2-3 cm longae, adpresse puberulae. Bracteae euphylloideae 2-3 cm longae, bracteolae anguste lineares, 1-3 mm longae, puberulae. Pedicelli 0.5-1.5 mm longi. Calycis tubus 1-1.5 mm longus ovatus puberulus vel glabrescens, lobi 4-5, triangular-lanceolati, obtusi 0.3-0.5 mm longi, tubo calycis 3-4 mm longi, sparse pilosi vel glabrescentes, septicide dehiscentes. Corollae tubus 10-12 mm longus, glaber, lobi 2-3 mm longi, glabri, antherae 2-2.5 mm longae. Semina oblonga usque ad 1.5 mm longa, apice tenuiter alata, basi vel basim versus lateraliter caudata, brunnea.

Syn.: Exostema elegans Alain Fl Cuba 5. 25. 1962, p.p. non Kr. et. Urb.
Holotypus: ACUÑA 10218 LS (HAC); Prov. Oriente; bordes del Rio Portillo,

Sierra Maestra, Pico Turquino, 26. 10. 1936. Isotypus: Herb. ROIG 7742 (HAC).

Specimina examinata: Prov. Oriente, Santiago de Cuba; La Julia, 900 m de alt. Leg.: G.B. BUCHER 11. 12. 1929; - Herb. ROIG 4948 (HAC); - Sierra Maestra, Loma del Gato, CRYSOGÓNE 4791; aug 1945; - CLEMENTE 5115; julio, 1946. - HIORAM 7622.

- ssp. eggersii (Urb.) Borhidi comb. et stat. novus

Basionym: Exostema eggersii Urb. Sym Ant. 9: 521. 1928.

Syn.: Exostema parviflorum Standl. N. Amer. Fl. 32: 124. 1921. non L. C. Rich.

Exostema parviflorum L.C. Rich. ssp. eggersii (Urb.) Borhidi Bot. Közl. 61: 157. 1973.

A typo differt foliis 5-10 cm longis, domatiis plerumque absentibus, subtus nervibus reticulato-conjunctis conspicuis.

Typus: EGGERS 4809 Santiago de Cuba (destruido en B).

Lectotypus: LEÓN 11958 Mesa de Prada Jauco, 17. Julio - 4 agosto 1924. HAC; isolectotypi: NY, US;

Specimina examinata: UO 2438, prov. Oriente, Guantanamo, Farallón La Perla, 28. 12. 1960. Leg.: LOPEZ FIGUEIRAS. - Zona de Moa, Baracoa, BUCHER 1005; - Sierra de Imias, monte fresco, LEÓN 12177; LEÓN 12232; - Altos del Rio Yumuri, Baracoa, LEÓN 17239; Valle del Rio Yumuri, Baracoa, LEÓN 17917. Daiquiri ad Papaya, Ekman 8389, Santiago, Britton et al. 12836.

- ssp. parvifolium Borhidi et Fernandez ssp. nova

A typo differt foliis ellipticis, oblongo-ovatis vel lanceolatis, 2-3.5 cm longis et 0.8-2.5 cm latis, 2.5-4 mm longe petiolatis, laminis folii subtus valde domatiatis et brevissime puberulis, nervis lateralibus 4-5, inflorescentiis puberulis, capsula glabra, seminibus 2-3 mm longis.

Holotypus: HAJB 22258; Cuba, Prov. Oriente, Palenque, Cuchillas de Toa, Cayo Fortuna, pinares y charrascos en el trillo de Riito a Piloto Arriba. Col.: BISSE et BERAZAIN, apr. 1972.

- ssp. wrightii (Kr. et Urb.) Borhidi comb. et stat. novus

Basionym: Exostema wrightii Kr. et Urb. in Urb. Symb. Ant. 1: 424. 1899.

Syn.: Exostema parviflorum Standl. N. Amer. Fl. 32: 124. 1921 p.p.-

Exostema parviflorum Alain Fl. Cuba 5: 25. 1962. p.p.

Exostema parviflorum L.C. Rich. ssp. wrightii (Kr. et Urb.) Borhidi Bot. Közl. 61: 157. 1973.

A typo differt foliis basi rotundatis, subcordatis vel truncatis, limbo leviter bullato, nervis lateralibus valde impressis et subtus puberulis, calyce puberulo vel dense pubescenti.

Typus: WRIGHT 2672; Cuba orientalis, cerca de Baracoa;

Specimina examinata: Yunque de Baracoa, ALAIN et LÓPEZ FIGUEIRAS 7245, 02. 01. 1960. MATIAS YERO 644; octubre 1965; - Farallones de Maguana, Baracoa, UO 594, LOPEZ FIGUEIRAS 10. 04. 1960.

21. Exostema pervestitum Borhidi et Fernandez sp. n.

Frutex usque ad 3 m altus. Rami hornotini teretes, puberuli vel breviter hirsuti, veteriores longitudinaliter striati, glabri. Stipulae interpetiolares late triangulares, apice rotundatae, brevissime mucronatae, basi connatae, 1-1.5 mm longae, lateraliter membranaceae, patentes, dorso hirsutae, caducae. Folia ovata, 1-2 mm longe petiolata, basi cordata vel rotundata, apice attenuata et obtusa, 2.7-6.0 cm longa et 1.5-4.0 cm lata, nervo medio supra impresso, subtus prominenti, lateralibus utroque latere 3-5, supra impressis, subtus prominulis et arcuatis, lamina supra breviter tomentosa et pallida, posterius glabrescens et nitidula, subtus velutina et in axillis nervorum lateralium arachnoideo-tomentosa, pallida, margine plerumque plana, membranacea vel chartacea.

Inflorescentiae corymbosae, multiflorae, sessiles 1.5-2 cm longae, 2.5-3.5 cm latae, hirsutae. Bracteae triangulares, 1-1.5 mm longae, bracteolae membrabaceae, squamiformes, minutae et basi hirsutae, apicem versus glabrae. Rami corymbi 0.5-1.5 mm longi, hirsuti, pedicelli 1-2 mm longi. Calycis tubus ellipticus, 2 mm longus, pubescens, lobi 5, triangulares, centripetaliter curvati, 0.5 mm longi, puberuli. Corollae tubus 5-6 mm longus, sparse pilosus, lobi 5, 2-3 mm longi, stamina exserta, antherae lineares, 2 mm longae. Capsula elliptica, non angulata vel costata, 3 mm longa, dense pubescens. Semina 2-5 per locula, circumcirca alata, basi breviter caudata, 1 mm longa.

Holotypus: LEÓN 18964 HAC. Prov. Oriente: Vertientes, Maisi. Leg.: LEÓN/ MATOS, April, 1939. HAC; Isotypus: NY.

Specimina examinata: ACUÑA, 17242, HAC, Farallones de Montecristo, Maisi, Febrero, 1929; LEÓN 11850 HAC, Oriente, Caleta al Este de Jauco, Cueva de Toro, Julio-Agosto, 1924; LEÓN 11853 HAC, Oriente, Costa al Este de Jauco, Julio-Agosto 1924; LEÓN 18569 HAC, Rio Maya, Maisi, October, 1938; ALAIN 5097 HAC, Abra de Yumuri, Baracoa, ALAIN et MORTON, 13. 01. 1956.

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Acta Botanica Hungarica 35(1-4), pp. 309-312 (1989)

STUDIES ON RONDELETIEAE (RUBIACEAE) XI; CRITICAL NOTES ON SOME CENTRAL AMERICAN SPECIES OF RONDELETIA S.L.

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Vácrátót

Studies carried out in the Herbarium of Missouri Botanical Garden (MO) on further Central American taxa classified into the genus Rondeletia L. permitted to make some new taxonomic decisions. Among the investigated 21 taxa of Rondeletia s.l. 19 proved to belong to the genus Arachnothryx Planch. and 2 to Rogiera Planch. The correspondent nomenclatural changes are composed in the article.

Separation of Arachnothryx from Rondeletia was suggested at first by STEYERMARK (1967) for the South American taxa and later by BORHIDI (1982) for the Central American species. The author of this paper strengthened to make further distinctions at generic level revalidating the genus Rogiera (BORHIDI, 1982) and describing a new genus, Javorkaea (BORHIDI and JÁRAI-KOMLÓDI, 1983). These taxonomic decisions has been recently supported by the karyological studies of KIEHN (1988), who found different basic numbers in Arachnothryx (x = 9), Rogiera (x = 10) and Rondeletia (x = 11).

According to these results a number of new combinations was suggested (BORHIDI, 1982, 1987). One of them later turned to be not correct. Namely Rondeletia hameliifolia Dwyer and Haydon of Panama is a really good Rondeletia s. str. and not an Arachnothryx as it was proposed by BORHIDI (1982).

Some new combinations in the genus Rondeletia related to
Central American taxa:

Arachnothryx albida (Lundell) Borhidi comb. nova - Mexico.
Basionym: Rondeletia albida Lundell Wrightia 5(8): 323. 1976.

Akadémiai Kiadó, Budapest

Arachnothryx acimunata (Oerst. ex Standl.) Borhidi comb. nova.

Basionym: Sommera acuminata Oerst. ex Standl. in J. Wash. Acad. Sci. 17: 340. 1927.

Syn.: Rondeletia mexiae Standl. Publ. Field. Mus. Nat. Hist. Chicago, Bot. Ser. 22: 55 1940. - Arachnothryx mexiae (Standl.) Borhidi Acta Bot. Hung. 33: 302 (1987) 1989.- Rodeletia acuminata (Oerst ex Standl.) Lorence et Castillo-Campos Biotica 17: 147. 1988.

Arachnothryx belizensis (Standl.) Borhidi var. longiloba (Lundell) Borhidi comb. nova - Mexico.

Basionym: Rondeleti belizensis Standl. var. longiloba Lundell in Wrightia 5(8): 323. 1976.

Arachnothryx falciformis (Lundell) Borhidi comb. nova - Mexico.

Basionym: Rondeletia falciformis Lundell in Wrightia 5(8): 324. 1976.

Arachnothryx longipetiolata (Lundell) Borhidi comb. nova.

Basionym: Rondeletia longipetiolata Lundell in Wrightia 5(8): 325. 1976.

Arachnothryx minor (Lundell) Borhidi comb. nova - Mexico.

Basionym: Rondeletia minor Lundell in Wrightia 5(8): 326. 1976.

Arachnothryx myriantha (Standl. et Steyerm.) Borhidi var. armentalis (L.O. Wms.) Borhidi comb. nova.

Basionym: Rondeletia myriantha Standl. et Steyerm. var. armentalis L.O. Wms. in Phytologia 26(2): 127. 1973.

Arachnothryx nicaraguensis (Oerst.) Borhidi comb. nova.

Basionym: Rondeletia nicaraguensis Oerst. in Kjobenhav. Vidensk. Meddel. 1852: 43.

Arachnothryx nitida (Hemsley) Borhidi comb. nova - Mexico.

Basionym: Rondeletia nitida Hemsley in Diagn. Pl. Nov. 1879: 29.

Arachnothryx ovandensis (Lundell) Borhidi comb. nova.

Basionym: Rondeletia ovandensis Lundell in Wrightia 5(8): 326. 1976.

Arachnothryx polycephala (Standl.) Borhidi comb. nova.

Basionym: Rondeletia polycephala Standl. in J. Wash. Acad. Sci. 17: 337. 1927.

Arachnothryx pyramidalis (Lundell) Borhidi comb. nova.

Basionym: Rondeleia pyramidalis Lundell in Wrightia 5(8): 327. 1976.

achnothryx rubens (L.O. Wms.) Borhidi comb. nova.

Basionym: Rondeletia rubens L.O. Wms. in Phytologia 26(2): 128. 1973.

achnothryx silvicola (L.O. Wms.) Borhidi comb. nova.

Basionym: Rondeletia silvicola L.O. Wms. in Phytologia 28(2): 128. 1973.

achnothryx tuxtlensis (Lorence et Castillocampus) Borhidi comb. nova.

Basionym: Rondeletia tuxtlensis Lorence et Castillo-Campos in Biotica 13: 148. 1988.

achnothryx urophylla (L.O. Wms.) Borhidi comb. nova.

Basionym: Rondeletia urophylla L.O. Wms. in Phytologia 28(2): 129. 1973.

achnothryx uxpanapensis (Lorence et Castillo-Campos) Borhidi comb. nova - Mexico.

Basionym: Rondeletia uxpanapensis Lorence et Castillo-Campos Biotica 13: 150. 1988.

rachnothryx wendtii (Lorence et Castillo-Campos) Borhidi comb. nova - Mexico.

Basionym: Rondeletia wendtii Lorence et Castillo-Campos in Biotica 13: 154. 1988.

rachnothryx yucatanensis (Lundell) Borhidi comb. nova.

Basionym: Rondeletia yucatanensis Lundell in Wrightia 5(8): 329. 1976.

ogiera seleriana (Loesener) Borhidi comb. nova.

Basionym: Rondeletia seleriana Loes. in Verh. Bot. Verein. Brandbg. 65: 105. 1913.

ogiera subscandens (Lundell) Borhidi comb. nova - Mexico.

Basionym: Rondeletia subscandens Lundell in Wrightia 5(8): 328. 1976.

Acknowledgements

The author expresses his thanks to the director of the Missouri Botanical Garden, Dr. Peter RAVEN, and to Dr. A. SOLOMON, the keeper of the Herbarium for the support of this work.

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Acta Botanica Hungarica 35(1-4), pp. 313-320 (1989)

EL HERBARIO JIMENO

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(Recibido: 12. Junio, 1988)

The Jimeno Herbarium has 2795 specimens of phanerogams collected by CHARLES WRIGHT in Cuba between 1856 and 1867. It was kept at the Instituto de Segunda Enseñanza, Matanzas, for about 65 years, and actually it is deposited in the Herbarium of the Cuban Academy of Sciences (HAC). Biographical data concerning F. DE JIMENO y FUENTES and a discussion of the taxonomic difficulties encountered during the revision of this new acquisition of the HAC are given.

Introduccion

La ciudad de Matanzas desempeñó un importante papel en la cultura cubana durante el siglo XIX, por lo que se le conoce desde entonces bajo el sobrenombre de "La Atenas de Cuba". Entre las figuras relacionadas con el campo de la ciencia que se destacaron en esa etapa está FRANCISCO DE JIMENO Y FUENTES (en algunos documentos antiguos el apellido se escribía Ximeno).

FRANCISCO DE JIMENO Y FUENTES nació en Matanzas, el 25 de julio de 1825. Perteneció a una familia acaudalada, lo que le permitió seguir estudios de Jurisprudencia en La Habana, los cuales no terminó, porque sentía preferencia por otras ramas del saber. Visitó Estados Unidos y Europa (1849-1951), como estudioso de la Historia Natural, la Arqueología y la Numismática. En esa época comenzó la confección de un museo particular, puesto que sentía una fuerte vocación por las ciencias naturales a históricas de su país. En 1851, a la muerte de su padre, se hace cargo de la administración de los bienes familiares y se interesa aún más en le Historia Natural, la Historia de Cuba y de América, la Economía, la Agricultura, etc.

Debido a esto, se relacionó con Sebastián alfredo de morales, JUAN GUNDLACH, FELIPE POEY, ANTONIO BACHILLER Y MORALES y fue el iniciador en los quehaceres científicos de CARLOS DE LA TORRE Y HUERTA. JIMENO estaba muy interesado en llevar a su ciudad natal y a su país los avances científicos de la época, por lo que se dió a la tarea de organizar su museo (Museo de Jimeno) el cual mantuvo canje de ejemplares con instituciones extranjeras.

Akadémiai Kiadó, Budapest

Por medio de GUNDLACH, compró un herbario colectado por C. WRIGHT, el cual formó parte del Museo. En la Exposición Universal de París, en 1867, GUNDLACH fue comisionado para llevar las valiosas colecciones de JIMENO a la Exposición, donde fueron premiadas. El objetivo de JIMENO era que se conociera el desarrollo alcanzado por Cuba en las ciencias.

Este "modesto obrero de la ciencia" (así le llamó CARLOS DE LA TORRE Y HUERTA) murió en Matanzas el 11 de febrero de 1890.

Según los Anales de la Academia de Ciencias de Cuba (22/2/1891), el Dr. EDUARDO DÍAZ, director del Instituto de Matanzas, íntimo amigo de JIMENO, reunió todos los restos dispersos de la Biblioteca y del Museo en el Instituto del cual era director, y fue por mediación de él que CARLOS DE LA TORRE pudo ceder a la Academia en aquella época las colecciones de fósiles y antigüedades únicas en Cuba.

Las colecciones de C. WRIGHT permanecieron en el Instituto de Segunda Enseñanza de Matanzas durante más de 65 años, en condiciones favorables de conservación y sólo respaldadas por dos números: el de colecta, dado por WRIGHT, escrito en sus etiquetas y con anotaciones en algunos casos, y el de la "Flora Cubana" (1873), dado por SAUVALLE. No obstante, este herbario nunca fue revisado por ninguno de los botánicos cubanos ni tampoco por los especialistas interesados en la flora de nuestro país.

Fue después que, al inicio de la fundación de la nueva Academia de Ciencias de Cuba (1962), el Herbario JIMENO (WRIGHT) fue transladado a la Academia con la finalidad de incorporarlo al resto de los herbarios que se encontraban en el antiguo Departamento de Botánica de la Estación Experimental Agronómica, atendidos por el Ing. JULIÁN ACUÑA, el cual comenzó a procesarlo, en la etapa de su jubilación, conjuntamente con la Lic. MILAGROS MONCADA, que trabajaba en ese Departamento.

Este herbario representa uno de los lotes en que fue dividido el material colectado por C. WRIGHT y para el Instituto constituye una valiosa adquisición; por tanto, el objetivo de este trabajo fue procesarlo, ordenarlo e identificarlo con el fin de incorporarlo a la sección histórica del Herbario de la Academia de Ciencias de Cuba (HAC) en condiciones de ser utilizado por los especialistas. Estos fueron los deseos de J. ACUÑA.

Materiales y Metodos

Al llegar al antiguo Departamento de Botánica, el material fue ordenado por familias, según el sistema de A. ENGLER, permaneciendo así durante algunos años. Posteriormente, fue envenenado y montado en cartulinas reglamentarias, manteniéndose en las mismas camisas numeradas. El material, ya preparado, fue reordenado por familias en nuevas camisas y de esta forma ACUÑA inició la identificación de los ejemplares. Como bibliografía básica se utilizó Plantae Wrightianae e Cuba Orientali (1860-62), Catalogus Plantarum Cubensium (1866), Flora Cubana (1873), y la Flora de Cuba (1946, 1951, 1953, 1957, 1964).

Siempre que se determinaba un ejemplar, se comparaba con su homólogo del Herbario SAUVALLE (WRIGHT) y se verificaba la numeración de WRIGHT y la de SAUVALLE. De esta manera, quedaba confirmada la identidad de los ejemplares.

A la muerte de ACUÑA (1973) la labor de identificación no se interrumpió y, aunque no en forma sistemática, se continuó con este trabajo con el mismo método que se había iniciado.

En algunos casos en que aparecían dos ejemplares de diferentes táxones, montados en una misma cartulina (mezcla de material), se buscaba la identidad de los mismos teniendo en cuenta la numeración de Wright.

Si no era posible la identificación de un ejemplar, se separaba y se consultaba con los especialistas.

El Herbario Jimeno está identificado mediante etiquetas que dicen: "Herbario CH. WRIGHT (de JIMENO), Academia de Ciencias de Cuba", y en los datos se da a conocer el número de WRIGHT, el nombre dado por GRISEBACH (o por WRIGHT), y el nombre actualizado en el caso de que exista. En el caso especial de las pteridófitas, se da el nombre adjudicado por GRISEBACH.

En la parte superior de las cartulinas se colocaron sobres en los que se incluyeron las etiquetas originales de WRIGHT con los números que las acompañaban y fragmentos de los ejemplares.

Las localidades y fechas se obtuvieron en algunos casos de las anotaciones personales de WRIGHT, y en su mayoría de las referencias básicas mencionadas y de "A summary of CHARLES WRIGHT's explorations in Cuba" (L.M. UNDERWOOD, 1905).

Resultados y Discusion

El Herbario JIMENO que hemos recibido está integrado solamente por criptógamas vasculares (pteridófitas) y fanerógamas (gimnospermas y angiospermas) con un total de 2795 ejemplares, lo que hace pensar que WRIGHT, aunque colectó criptógamas no vasculares, no dejó duplicados en Cuba. Según LEÓN (1939), en el Herbario Sauvalle, homólogo del Herbario JIMENO, faltaban las criptógamas no vasculares y algunas familias de angiospermas, por lo que agregó números de La Salle con el fin de completar los táxones no presentes.

Este herbario consta de 373 criptógamas vasculares y de 2422 fanerógamas. En la Tabla 1 se da la relación por familias, número de ejemplares, géneros y especies respectivamente.

Comparando este herbario con el de SAUVALLE (WRIGHT), 18 familias no están representadas en JIMENO (WRIGHT); no obstante, están presentes 11

Tabla 1

Relación por familias, número de ejemplaes, géneros y especies, respectivamente del Herbario JIMENO

Familia	No. de ejem- plares	No. de géneros	No. de especies
Cycadaceae	2	1	2
Podocarpaceae	4	1	2
Pinaceae	5	1	1
Cupressaceae	2	1	1
Potamogetonaceae	6	1	4
Najadaceae	1	1	1
Butomaceae	1	1	1
Alismataceae	8	2	4
Poaceae	68	26	39
Cyperaceae	34	8	19
Arecaceae	1	1	1
Araceae	6	3	5
Lemnaceae	2	1	1
Mayacaceae	4	1	1
Xyridaceae	4	1	2
Eriocaulaceae	17	4	7
Bromeliaceae	21	5	12
Commelinaceae	4	2	2
Pontederiaceae	17	4	9
Juncaceae	2	1	1
Smilacaceae	7	1	4
Haemodoraceae	5	2	2
Amaryllidaceae	9	5	5
Agavaceae	1	1	1
Dioscoreaceae	13	2	7
Iridaceae	2	1	1
Zingiberaceae	8	3	3
Cannaceae	3	1	1
Marantaceae	5	1	1
Burmanniaceae	10	4	5
Orchidaceae	100	27	66
Piperaceae	22	3	20
Chloranthaceae	1	1	1
Salicaceae	1	1	1
Myricaceae	1	1	1
Picrodendraceae	1	1	1
Fagaceae	2	1	1
Ulmaceae	6	3	5
Moraceae	12	6	10
Urticaceae	28	7	24
Loranthaceae	32	4	16
Olacaceae	5	2	3
Balanophoraceae	1	1	1
Aristolochiaceae	7	1	5
Polygonaceae	13	2	13
Chenopodiaceae	1	1	1
Amaranthaceae	11	6	6

Tabla 1 (Continuación)

Familia	No. de ejemplares	No. de géneros	No. de especies
Nyctaginaceae	15	3	5
Phytolaccaceae	2	2	2
Aizoaceae	7	3	3
Portulacaceae	3	2	3
Caryophyllaceae	2	1	2
Nymphaeaceae	3	3	3
Ranunculaceae	3	2	3
Menispermaceae	4	2	2
Magnoliaceae	3	1	1
Illiciaceae	2	1	1
Annonaceae	10	5	6
Lauraceae	33	6	12
Papaveraceae	2	1	1
Brassicaceae	4	2	3
Capparaceae	12	3	8
Droseraceae	4	1	2
Podostemaceae	2	1	1
Brunelliaceae	1	1	1
Rosaceae	5	3	3
Connaraceae	4	3	3
Mimosaceae	11	5	11
Caesalpiniaceae	22	6	20
Fabaceae	49	29	43
Oxalidaceae	4	1	2
Erythroxylaceae	11	1	1
Zygophyllaceae	1	1	1
Rutaceae	19	6	15
Simaroubaceae	8	4	5
Burseraceae	7	2	5
Meliaceae	7	2	3
Malpighiaceae	23	5	12
Polygalaceae	21	2	11
Dichapetalaceae	2	1	1
Euphorbiaceae	162	31	91
Buxaceae	4	1	3
Anacardiaceae	8	4	7
Cyrillaceae	5	2	3
Aquifoliaceae	16	1	5
Celastraceae	40	6	15
Hippocrateaceae	4	3	3
Staphyleaceae	1	1	1
Icacinaceae	4	2	2
Sapindaceae	42	8	14
Sabiaceae	2	1	1
Rhamnaceae	18	4	11
Vitaceae	3	2	3
Elaeocarpaceae	5	2	3
Tiliaceae	7	5	6
Malvaceae	50	12	27
Bombacaceae	5	2	2

Table 1 (Continuación)

Familia	No. de ejemplares	No. de géneros	No. de especies
Sterculiaceae	14	4	10
Dilleniaceae	8	4	4
Ochnaceae	12	2	7
Theaceae	10	3	5
Clusiaceae	9	4	6
Hypericaceae	11	1	6
Elatinaceae	2	1	1
Cochlospermaceae	4	1	1
Canellaceae	2	1	1
Violaceae	2	1	1
Flacourtiaceae	53	10	25
Turneraceae	3	1	2
Passifloraceae	8	1	5
Begoniaceae	6	1	4
Cactaceae	8	5	5
Thymeleaceae	11	3	6
Lythraceae	19	4	10
Rhizophoraceae	2	1	1
Combretaceae	15	7	9
Myrtaceae	58	9	44
Melastomataceae	113	14	73
Onagraceae	8	3	8
Haloragaceae	2	2	2
Araliaceae	5	2	2
Apiaceae	4	1	3
Cornaceae	2	1	1
Clethraceae	2	1	1
Ericaceae	22	5	10
Myrsinaceae	8	5	7
Theophrastaceae	6	2	3
Primulaceae	2	1	2
Sapotaceae	13	5	11
Ebenaceae	5	1	4
Styracaceae	1	1	1
Symplocaceae	4	1	4
Oleaceae	7	2	5
Loganiaceae	5	4	4
Gentianaceae	11	9	9
Apocynaceae	39	11	21
Asclepiadaceae	24	7	16
Convolvulaceae	43	7	27
Hydrophyllaceae	5	2	3
Boraginaceae	57	6	30
Verbenaceae	49	13	30
Lamiaceae	29	7	15
Solanaceae	31	7	19
Scrophulariaceae	31	11	23
Bignoniaceae	35	11	18
Gesneriaceae	24	4	13
Lentibulariaceae	6	1	4

Table 1 (Continuación)

Familia	No. de ejemplares	No. de géneros	No. de especies
Acanthaceae	37	10	22
Rubiaceae	249	52	127
Valerianaceae	2	1	1
Cucurbitaceae	11	6	6
Campanulaceae	10	3	6
Asteraceae	65	29	53

familias que según LEÓN (1939) faltaban en el material de SAUVALLE, por lo que desconocemos si, a pesar de su buen estado de conservación, ha habido pérdida de materiales en el Herbario JIMENO.

Conclusiones

- Se recuperan isótipos de muchas especies de GRISEBACH, de WRIGTH, y de otros botánicos que colaboraron en la identificación del material wrightiano.

- Se recuperan algunos ejemplares de los cuales sólo se contaba con fotótipos o duplicados del New York Botanical Garden.

- Se recuperan táxones que no están presentes of fueron destruidos en el Herbario SAUVALLE (WRIGHT): Tiliaceae, Malvaceae, Nymphaeaceae, Menispermaceae, Ranunculaceae, Magnoliaceae, Annonaceae, Myrsinaceae, Primulaceae, Gesneriaceae, y Sterculiaceae.

- Se concluye que, ya que el Herbario SAUVALLE y el Herbario JIMENO se complementan, el HAC posee en la actualidad una collección wrightiana bastante completa, en la cual están representadas todas las familias de imortancia colectadas ya desde el siglo pasado.

- FRANCISCO DE JIMENO Y FUENTES tiene el mérito en el ámbito de la Botánica, de haber logrado consequir y mantener una de las más valiosas colecciones de plantas colectadas en el siglo pasado y de haberlas incorporado a su museo. Esta constituye la segunda colección de plantes wrightianas que se conservan en Cuba.

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Acta Botanica Hungarica 35(1-4), pp. 321-332 (1989)

BOOK REVIEWS

ed.: Z. SZŐCS

WIESSNER, W. - ROBINSON, D.G. - STARR, R.C. (eds): Algal Development. Molecular and Cellular aspects. - Springer-Verlag, Berlin, Heidelberg, New York, 1987. p. 188

This book is the proceeding of the Third Symposium on Experimental Phycology, held in September 1986 in Göttingen, under the auspices of the Akademie der Wissenschaften in Göttingen. The authors inform us about that... "In recent years our understanding of the molecular basis of cellular development has advanced significantly. At the same time algae have become more and more favoured for a whole range of studies in related areas of biology." This is well-demonstrated by the fact that the representatives of almost all algae phyla are present in the 20 articles. The most frequent objects of research are the Phytomonadia species, especially the **Chlamydomonas** species among them.

Thought the title of the symposium suggests coherent material, the articles comprise a wide range. It might be advisable to do some classification among the articles. The first 5 works connect to the theme of cell-division. EDMUNDS, JOHN, TISCHNER and LORENZEN write about the timer control of cell-division, about the circadian rhythm based on experiments with Euglena, Chlamydomonas, Chlorella species. PICKETT-HEAPS and SCHMID's articles are on diatoms. The first one is on a model system of mitosis in Pennales species (Diatom mitosis: Implication of a model system), while the second one is on the morphogenesis of the cell-wall in Thalassiosira and Coscinodiscus species. The works of GILLES et al., WENZL and SUMPER, MAIER, SCHLÖSSER, MUSGRAVE, ADAIR, MELKONIAN et al. can be grouped into the topic of sexual reproduction. A third group of the articles deals with the functioning and structure of the chloroplast and its processes of protein synthesis. Certainly, some articles are missing from this partially arbitrary classification - those are also part and parcel of the book, making it more colourful.

I would like to appreciate PICKETT-HEAPS, SCHMID, MUSGRAVE, MELKONIAN et al.'s works, which rightly can draw the attention of researchers of algae taxonomy onto them. The results on mitosis of diatoms and their wall-morphology, and on the development-function of the flagella of Chlamydomonas, Nephroselmys species are very interesting from taxonomic point of view as well. The comprehensive results of JOYARD et al. on the glicerolipid constitution of the membranes of certain procariots (Cyanobacteria), eucariot algae and higher plants are worth attention, too.

The book edited by WIESSNER, ROBINSON and STARR is a thorough, authentic work with several outstanding articles. The LM, TEM, SEM micrographs, the figures and photographs supplementing certain articles are of high standard press-work. The book is recommended to all botanists, algologists whether working in cell-morphology, physiology or biochemistry. It can be equally important in university education as well.

K.T. KISS

HINDÁK, F.: Studies on the Chlorococcal Algae (Chlorophyceae). IV. Veda, Biol. Práce, Bratislava, 1988. p. 263

We can get the most precise informationon the aim of HINDÁK's book from a part of its preface. "As the three preceding Studies on Chlorococcal Algae published in 1977, 1980 and 1984, this fourth Studies are also devoted to the morphological variability and taxonomy of coccal green algae (Chlorophyta), drawing immediately on them both in term of form and content. What we deal here with are both hitherto not found algae and such that had previously already been studied and are now completed by new findings. More attention than hitherto has been paid to species multiplying by zoospores. Because of the considerable treatises published in recent years, knowledge of this group of algae augmented markedly, as borne out also by the

recently published monograph on Chlorococcales written by the Czechoslovakian authors Dr. J. KOMAREK and Professor B. FOTT (1983). In spite of this, many questions remain open and unsolved in the taxonomy of Chlorococcal algae. These Studies aim at contributing to their elucidation."

The book describes the species of 7 families in the Chlorococcales order. It reports on 10 new genera (Ferricystis, Ettliella, Siderocoelopsis, Cylindrocelis, Podohedriella, Kirchneria), 19 new species and 65 new combinations altogether. It is apparent that HINDÁK's work is a significant one and none of the algologists should lack for it. Especially, when we take into consideration that in the 92 plates there are far more that 1000 well-made algae drawings. Nowadays, when algae taxonomy is in upheaval, this kind of profound works enhance the clarification of the principles of classification and the accomplishment of a summarizing, critical work.

HINDÁK's book which is a due continuation of the first three volumes of the series is warmly recommended to every algologist and hydrobiologist working in theoretical or practical fields. The book which contains 98 references to the literature and is supplemented with an English, Slovakian and Russian summary and an object index will most probably be one of the most often used works of algology.

K.T. KISS

ETTL, H. - GARTNER, G.: Chlorophyta II. Tetrasporales, Chlorococcales, Gloeodendrales. In: Ettl, H., Gerloff, J., Heynig, H., Mollenauer, D. (eds): Süsswassserflora von Mitteleuropa. Band 10., G. Fischer Verlag. Stuttgart, New York, p. 436

Among the 24 volumes of "Süsswasserflora von Mitteleuropa" 9 were devoted to the Chlorophyta phylum by the editors. In the 2nd volume 3 genera of the phylum is discusssed by the authors - one of them, HANUS ETTL we have met already as the author of the books Xanthophyceae I. and Chlorophyta I. Phytomonadina.

The editors' preface is followed by the authors' preface, which acquaints us with the inner structure of the book and with the morphological features and points why these three orders are discussed together in the same volume.

Interestingly, the taxonomic-key makes possible the determination only of 13 classes which is a "reduction" comparing to the volumes appeared after 1984, where a key to 20 algae classes were presented. Among these were the Chlamydophyceae and Chlorophyceae classes (the orders of both classes are involved into the 9th and 10th volumes). With the taxonomic key in the present work one can go till the Chlorophyceae class and then find a note on the more detailed classification included in the 9th volume. This should have been adopted into the present volume too, since 2 out of the 4 orders of the Chlamydophyceae class and 1 order of the Chlorophyceae class were included into the 9th, while the 2 other orders of the Chlamydophyceae class and 1 order of the Chlorophyceae class into the 10th volume. This way the latter work would have been more complete.

This type of "back and forth references" might be expected in all the 9 Chlorophyta volumes - we would welcome those. It also would be more comfortable if for the general description of the Chlorophyta phylum we did not have to reach out for the 9th volume.

The general description of the Tetrasporales order gives insight into the structure of the cell-wall and the covering jelly, the protoplast, the chloroplast and the pulsing vacuole, into the asexual and sexual reproduction ways and into general taxonomic concerns. This is followed by taxonomic keys to the three families of the order and short descriptions of the families.

After it comes the key to genera, which is supplemented with drawings summarizing the main features of the genera. All these are followed by the key to species and the detailed description of each species. Excellent drawings - often 4-5 to a single species - makes the presentation of the morphological characteristics complete. The descriptions are complemented with data on distribution and ecology.

In the Chlorangiellaceae family of the Tetrasporales order 10 genera and 39 species, in the Palmellopsidaceae family 9 genera and 29 species, in the Tetrasporaceae family 7 genera and 17 species are elaborated and approximately the same number of species with uncertain classification are listed and described briefly.

The general description of the Chlorococcales order is much more detailed than the previous one. The inner structure of the chapter is the same but at the end the authors write about the methods of culturing, studying and determining algae as well.

Within the order, in the Chlorococcaceae family there are 15 genera and 110 species, in the Characiochloridaceae 2 genera and 14 species, in the Actinochloridaceae family 5 genera and 21 the Actinochloridaceae family 5 genera and 21 species, and numerous uncertain species.

The brief general description of the Gleodendrales order of the Chlorophyceae class is followed by the key to its 3 families, its genera and species and by their descriptions.

In the Gloedendraceae family 7 genera and 8 species, in the Chaetopeltidaceae family 5 genera and 10 species and in the Characiosiphonaceae family 1 genus and 10 species are described.

The book ends with the references to the literature (to 135 works) and an object index.

The 311 figures practically mean more than 1000 drawings of algae.

The clear-cut make-up, the detailed morphological characterizations, the accurate descriptions of the species and the huge amount of drawings makes Ettl and GARNER's work a guide-book which can be used by all experts with good certainty. This brilliant book with high press-work standard is recommended besides algologists to all taxonomits, hydrobiologists and biologists working in water conservancy. Furthermore, it can be useful in university education and in all fields where the accurate identification of and knowledge about the species of the Tetrasporales, Chlorococcales and Gloeodendrales orders are needed.

K.T. KISS

HEGEWALD, E. - SILVA, P.C.: Annotated Catalogue of Scenedesmus and Nomenclaturally Related Genera, Including Original Descriptions and Figures. - Bibliotheca Phycologica, Band 80. J. Cramer, Berlin-Stuttgart, 1988. p. 587

The Scenedesmus genus is the most various and at the same time taxonomically very controversial group of the green algae, therefore this is one of the algae genera which most often appear in publications. The accumulated knowledge has been published in several monographs (G.M. SMITH, CHODAT, AHLSTROM, UHERKOVICH, KIRJAKOV), identification handbooks (KORSIKOV, KOMÁREK and FOTT) and many scientific publications. We have to admit that from the fifties, HORTOBÁGYI and UHERKOVICH's works enlarged the knowledge about the Scenedesmus species in natural waters with many Hungarian and numerous foreign (Brasilian, Vietnamese, African, Indian and North-European) data. Among the nearly 2000 names of the Scenedesmus nomenclature, roughly 340 originates from Hungarian authors, mainly from the above-mentioned ones.

This work on Scenedesmus appeared as the 80th volume of the Bibliotheca Phycologica is neither a monograph nor an identification handbook, rather a catalogue with notes on the Scenedesmus taxa published up to now. So it is a unique handbook, different from all the previous ones, the greatest credit of which is that it contains comprehensively the descriptions and other data of Scenedesmus taxa published up to now.

The book starts with a short historical review including all the significant events of Scenedesmus research. The second chapter tells about the structure and extent of the catalogue, the aim of the book and the ways of data-work up. As the authors indicate: "The catalogue includes all scientific names published in Scenedesmus, and in several other genera that are implicated in Scenedesmus taxonomy, whether valid or invalid." "For each entry of a new taxon is given the author, the place of original publication, a transcription of the original description or diagnosis, the type locality, the type, and a reproduction of the original illustrations (in part or in whole)."

In the case of uncertainties in the nomenclature, the aboves are supplemented with short taxonomic comments and opinions. Naturally, some of the opinions reflect the author's personal point of view.

In the third chapter P.C. SILVA analyses nomenclature problems indicating that the *Scenedesmus* scientific names very often neither follow the international rules (ICBN) nor the Latin grammatical laws. The latter refers specially to the extremely numerous intraspecific taxa - the author corrects the Latin grammatical mistakes at once.

The 557 page catalogue is supplemented with a short appendix referring to the most recent works not yet included in the book.

The catalogue - in accordance to its aim - contains all genus and almost all species names (including the intraspecific taxa, too) presented in the *Scenedesmus* nomenclature up to now, in an alphabetical order, complemented with high-standard copies of the original drawings. Above the *Scenedesmus* genus name, short chapters are devoted to the species/taxa *Achnantes*, *Arthrodesmus*, *Chlorella*, *Chlodatella*, *Coelastrum*, *Dicellula*, *Didymocystis*, *Didymogene*, *Enallax*, *Heterodesmus*, *Lagerheimia*, *Lauterborniella*, *Pseudotetradesmum*, *Raphidium*, *Raysiella*, *Schorederiella*, *Selenastrum*, *Steinedesmus*, *Steiniella*, *Tessararthra*, *Tessarthonia*, *Tetrachlorella*, *Tetradesmus*, *Tetrastrum*, *Trochiscia*, *Victoriella*. During past periods of algae research, some *Scenedesmus* species were classified into some of these genera (e.g. *Achnentes*, *Arthrodesmus*) because of various reasons - even in most recent times the *Scenedesmus* genus is not well marked off from other genera of the *Chlorococcales* order.

According to recent studies, some organisms described as *Chodatella* or *Laserheimia* species are nothing but unicellular *Scenedesmus*. In case of reclassification, the original drawing can be found at the basionym.

The division of the *Scenedesmus* genus into subgenera, sections, subsections and series reflects basically HEGEWALD's opinion.

The book is closed with an extremely rich reference to the literature (references to 416 works).

The specialist probably would be interested in the opinion of the author about some of the *Scenedesmus* taxa described from the territory of the Soviet Union and summarized in the book edited by GOLLERBACH (Vodorosli-Vid. BAN USSR, Leningrad, pp. 624, 1971). This book and most of the studies on which the book is based are not even mentioned by the author. We admit that it is not easy to make a decision in the case of many taxa presented in GOLLERBACH's work, but HEGEWALD should have at least mentioned them, since he aims for completeness.

The book is verily a useful one, though on the first place for such experts and researchers who has already acquired considerable knowledge in the topic. Mainly practised experts can benefit by the numerous notes on the synonyms and can integrate them in a critical way. This summarizing work based on light-microscopic data is a basic resources for further taxonomic studies since it contains the bulk of the original descriptions and drawings.

G. UHERKOVICH and A. SCHMIDT

KRAMMER, K. - LANGE-BERTALOT, H.: Bacillariophyceae, 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae, In: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (eds): Süsswasserflora von Mitteleuropa, Band 2/2, Fischer Verlag, Stuttgart, New York, 1988. p. 596

The highly successful first volume of this work appeared in 1986 - the continuation was eagerly waited. The structure of the second volume is naturally the same as the first one. The short prefaces by the editors are followed by a taxonomic key to 20 classes of algae. Based on the key, the class *Bacillariophyceae* can be easily and securely separated from other algae classes.

In the short introductory part there is a general description of the canal raphe families supplemented with a glossary of terminology. Unfortunately, the authors did not add a vocabulary of the English, French and Latin counterparts of the German terms as they did in the first volume.

The second chapter discusses the Bacillariaceae, Epithemiaceae and Suririllaceae families of the Pennales order. The general description of each family is followed by the key to the genera belonging to the given family, the general description of each genus and the keys to the species. Within the Nitzschia genus, the authors made a segregation of cohorts (e.g. Lanceolate, Tryblionellae). This enhances, in fact makes it possible to understand this genus made up of hardly distinctable species, and to determine its species accurately. After the keys to species comes the detailed description of the species, in several cases together with the presentation of the features of their electromicroscopic structure. All these are completed by a list of species of similar structures, synonyms, valuable taxonomic comments, data of distribution and some ecological concerns.

The species covered by the book distribute among genera as the following:

Bacillaria	1	Nitzschia	142
Hantzschia	11	Cymbellonitzschia	1
Cylindrotheca	1	Simonsenia	1
Denticula	7	Epithemia	9
Rhopalodia	8	Cymatopleura	3
Surirella	35	Stenopterobia	4
Campylodiscus	6		

The book contains 1914 photographs in 182 tables. The photographs can be mentioned only in the voice of the highest appreciation. Mainly in the discussion of the Nitzschia species with extremely fine structured shells and in several other cases too, the LM microphotoes are supplemented with SEM photographs in order to complete the text and ensure the accurate determination. The volume has a high-standard presswork like the first one had.

We are eagerly waiting for the third volume of the book by KRAMMER and LANGE-BERTALOT, partly to obtain the description of the missing genera and species, partly to have the references to the literature, since the lack of those unfortunately reduces the value of this excellent work. Besides algologists and diatomologists, we can recommend without hesitation the 2/2 volume of Bacillariophyceae to hydrobiologists working both on theoretical and practical fields. The book should not be missing from the bookshelfs of taxonomists and university teachers.

K.T. KISS

DAHLGREN, G.: Systematische Botanik (Systematical Botany). Springer-Verlag, Berlin-Heidelberg-New York-London-Paris-Tokyo, 1987. p. 258

The book gives an up-to-date, summarizing and accurate introduction into plant-systematics - it is an attempt to present a colourful picture of the topic, in spite of the restricted size. The reason why this book was written and translated into several languages is that a clear and considerably inexpensive text-book had been missing from the education of plant-systematics for many years. First of all, it can serve as an introduction to basic learnings of university and high-school level plant-systematics for all those students of biology who touch plant-systematics, history of cultivated plants or geobotany during their course of education. Furthermore, the book can be useful for secondary and primary school teachers as an introduction to the different chapters of special botany.

The aim of the authors was to give such a summary in plant-systematics which - on the one hand is built on new scientific results - on the other hand is dynamic and flexible. Among the newer systems, they chosed CRONIQUIST's (1968) and TAKHTAJAN's (1969), while knowing that the latter perhaps overemphasizes certain feature combinations.

The first chapters are devoted to the explanation of the terminology of plant-systematics, which is followed by a review on the history of plant-systematics and on the significance of the disciplines indispensable to up-to-date systematization. The classification

of the plant kingdom - which was based almost completely on the external morphology earlier - in recent years increasingly uses the results of other disciplines, such as anatomy, embr - ology, cytology, genetics, physiology and chemistry. Among these, cytological chemistry is specially important. The chemical compounds and their distribution in plants are important characteristics. Since identical products can be synthetized by completely different biosynthetic pathways, from phylogenetic point of veiw, not the end-products but the whole biosynthetic process has primary significance. Proteins are specially important since they directly reflect the DNA structure and activity. Until now, the varieties of a simple protein, the citochrom C were analysed from different genera of 25 seed-bearing plant species. The gained pattern of variability is not easily explainable but seems to support the present taxonomic order of the genera.

The following chapters are devoted to the different forms of reproduction, metageny, production economy and the energy/nutrient utilization of plants. A separate chapter introduces the taxonomic categories and terminology to the reader. Nearly 100 pages present the phyla of plant kingdom in details. They include theories on the origin of certain phyla, their cytological description, chromosoma numbers, life-cycles and morphology, their approximate species numbers, the list of the most important genera, and the description of the most important species. Latter is illustrated with excellent drawings.

The other theme of greatest extent is the morphology of Angiospermae; first the morphology of the juvenile plants, then the vegetative and generative organs of the plants are discussed from ontogenetic and morphologic points of view, together with their modifications. Regrettably, the work regarding leaf and flower morphology is not consize.

The chapter on systematics was written by considering the morphological characters and by using the principles of convergency and divergency and that the form of an organ is very variable in certain taxa, while relatively unchanging at other ones. Therefore, the systematic value of a certain character cannot be generalized to the whole Angiospermae system. The characters of vegetative and generative organs significant in systematization are listed with examples. Above the morphological characters, anatomical, chemical and cytological ones are presented, too.

The filogenetic and fenetic comparison of the Angiospermae system is followed by the discussion of the dicots. This chapter is a rather short one; it describes the most important families, and one species in each family.Similarly, the monocots are discussed very briefly, merely 5 pages are devoted to them. It is a pity, that in a university level text-book the material has to be shortened so much that several important taxa cannot be discussed.

To make the book complete, a chapter deals with cultivated plants, pollination and distribution biology, life-forms and the geobotany of the world, especially of Europe.

The structure and the chapters of the book are clear, the morphological characters illustrating the families and the evolutionary processes are well-understandable with the help of the numerous accurate drawings, figures and diagrams.

Botanists and botanical institutes, the medium and high level education should not lack for this excellent comparative work, which contains the latest results and theories. Study circles of biology can benefit by it as well. Both its content and get-up are so outstanding that all the opinions support its translation into Hungarian.

J. DARÓK

HAMEL, G. - WALTER, H.: Orchideen - Bildtafeln mitteleuropäischer Arten, Formen und Bastarde II. - VEB. G. Fischer, Jena. 1986, 32 tables, p. 63

The second volume of the picutre series of the orchids living in the territory of the German Democratic Republic contains the water-colour paintings of 25 less endangered taxa and their well-recognisable natural hybrids together with a one-page description of each plant. The series aims to give a popularizing presentation of the whole family and its genera while maintaining scientific character, and to help the identification by describing the plants' main features. Tough there is no room to present special local deviations or taxonomic curi-

osities, some bastard forms so much typical for the whole family cannot be excluded. In fact, it is a famous character of the family that natural hybridizations occur not only among species but among genera, too. Moreover, often threefold bastards are created by the hybridization of a hybrid and a third species.

Like in the first volume, a separate booklet contains the descriptions. In its preface, HAMEL, the leader of the East-German group of orchid-lovers brings the reader's attention to the most important points of the topic. In a separate chapter he discusses the recent problems of the protection of the family and the most urgent tasks connected with it. The descriptions written by well-known German experts provide detailed taxonomic analyses and ecological-coenological characterizations above the general morphological and phyto-geographical data. They pay special attention to the status in nature conservation of the discussed taxon on the basis of the latest Red List (KORNECK et al., 1984). A great merit of the descriptions is that the characters by which the differentiation from the closest relative taxon can be made are listed in details. The booklet ends with the list of localities, which makes the work more complete.

According to its goal, the series does not aim at completeness, still it can be useful for botanists and nature conservationists besides plant-lovers.

Z. KERESZTY

CHERNOV, I. YU.: The living tundra. Cambridge University Press, Cambridge, 1988. p. 213.

We had very few exact information so far about one of the most exciting geographical and botanical areas of the world, called tundra. This treeless landscape situated north of the taiga along the coast of the Arctic Ocean, and its islands.

The author has drawn a far-reaching picture of the life of this landscape. The book has 9 Chapters and an exhaustive bibliography.

CHERNOV is basically a naturalist, in the classical meaning of the word. He is first of all a discoverer of the "interrelationships between organisms" living on the tundra (Chapter 8).

No doubt all chapters are based on intensive field works. CHERNOV doesn't "playing" with the usual notions like "competition", "exclusion", "predation",etc., and he doesn't want to enforce a theroy on to the living organisms. He has kept a close watch on the specific types of food-webs of this area and he was able to construct a real view of the "infinitely variable interrelationships between organisms".

The paid attention to the ethology of the animals as well and at the same time he was able to show us the quantitative aspects of the food chains, both in the cases of producers, consumers, predators, necrophyges, saprophages and of phytophages. For instance, he estimated the number of nematodes per square metre in the soil, and the role of microscopic algae within the tundra associations. One of the most interesting results of CHERNOV's book is the highlighting of the relationship between the microphytophages and their food sources of algae. Latter constitutes the "basic part of the primary production". The very complex "teamwork" between algae and microphytophages and the relations between animals and lichens give the basic character of the ecology of the tundra.

The author has found connections between the different life forms of lichens and their consumption. Lichens are very nourishing, not only for reindeer, but for small invertebrates (e.g., mites or springtails), too. Dead particles of lichens provide food for saprophagous animals.

All chapters are full of examples. CHERNOV has made examinations about the pollination biology of entomophilous plants, too. It was found that in the "typical tundra", the general number of the species of entomophilous plants is approximately equal with the number of species of anthophilous insects. However, there are big differences between "artic tundra", "southerly zones", "coniferous forest" and "steppe meadows" in the case of the ratio between the species number of entomophilous plants and of antophilous insects. These investigations

have proved that the thorough examination of the insect-plants relations may give an important new aspect in the classification of plant communities. At the same time the results of these kinds of researches have pointed out that the simultaneous observations about the reproductive biology of plants and of the ethology of insects may serve a vigorous impact on the understanding of the structure and function of the biocoenoses.

The book contains 60 figures, including excellent photos. Especially the photos of the chapter, entitled "Adaptation of living organisms" are extremely expressive. They are in a good connection with the text, emphasizing the close connection between the sciences of ethology and ecology and of morphology and ecology. The usually applied rules in connection with adaptation, like Bergman's rule or Allen's axiom, are handled not in a categorical manner but always on the basis of the author's filed experiences.

Two main kinds of adaptation are presented in the book such as the "morpho-physiological" and "ecological-physiological' ones. One of the most interesting parts of this book is the explanation of the "passive ecological-physiological adaptation" which "... subjects the vital capacity of an organism to the surrounding environment and at the same time increases its resistance to unfavourable effects and promotes a more economic utilization of energy".

CHERNOV's book was first published in the USSR, in the year of 1980. This it the second edition in English. It's no doubt, CHERNOV's book is one of the most inventive among the recently published ones in the field of ecology.

This book should not be absent from the library of an ecologist, and is recommended for students and ethologists as well.

T. KISS

N, W.: Auswirkungen von Umweltchemikalien auf den Gaswechsel von Grünlandpflanzen. , Göttingen, 1987. p. 92

This booklet, No. XIII of the series Scripta Geobotanica, edited by the Department of Systematics and Geobotany of Göttingen University, is a thesis, but it forms a part of a greater program having the goal to find methods for the ecotoxicological evaluation of possibly dangerous chemicals. The problem dealt with here is whether the intensities of photosynthesis, dark respiration and transpiration can serve as indicators of early stage of intoxication, in this case caused by two model substances, atrazin and pentachlorophenol. Though experiments in greenhouse were also made, most of them were carried out in the open field, mainly in stands of Trifolium repens and Lolium perenne (mowed but not grazed) important components of North-Western Germany's meadows and pastures. To lesser extent other meadow plants were also studied, both in field and greenhouse.

Despite the conciseness of the descriptions, the methods (elaborated mainly in the FRG) deserve highly our attention. Field experiments were carried out by means of a modern and sophisticated mobile laboratory, equipped among others with a remarkably stabile new type IRGA apparatus, that needed calibration only once per four months. Air humidity and temperature within the cuvettes were regulated either to prescribed, fixed values or according to the outer weather circumstances allowing in this latter case to obtain data of really ecophysiological importance. The dynamics of the gas exchanges was followed continuously on about 250 days (i.e. during two seasons), so that an imposing mass of data was gathered and also analysed by means of the computer. In this way many sides of the normal ecophysiological behavior of the objects could be characterized, first of all the dependence of their gas exchange processes on the season and the environmental factors. This is one of the great merits of the book; its results in this direction are in themselves very valuable, not only as a basis of comparison with the injured state of the objects.

As pointed out by the author hismelf, when used to solve ecotoxicological problems, his methods have advantages and weaknesses. On the one hand, as documented in minute details, the dynamics of the injury and also of the recovery of the gas exchange processes can be fol-

lowed precisely and without delay, and also the differing sensitivity of the various species can be easily stated. On the other hand, the little number of the cuvettes permits to test only a limited number of chemicals and/or doses. In addition, the methods are laborious and expensive. Unfortunately no comparison is made with other possible ecotoxicological methods, and it is not said either whether the physiological processes studied are the most susceptible ones to ecotoxicological damages.

In particular because of its strong methodical background the book is warmly recommended to researchers interested in ecophysiological and ecotoxicological problems. It is written in an easily readable German with a short English summary.

L. PÓLYA

HUTCHINSON, T.C. - MEEMA, K.M. (eds): Lead, mercury, cadmium and arsenic in the environment. SCOPE Vol. 31. John Wiley, Chichester, New York, 1987. p. 360

This volume presents the SCOPE Metal Cycling Workshop which was held in Toronto, in September 1984. The workshop chaired by T.C. HUTCHINSON discussed four very significant environmental pollutants - arsenic, cadmium, lead and mercury. Part I covers the group reports of rapporteurs on the four elements and the need for standard reference material for metal analyses. Part II involves 16 papers of 21 contributors. Participants came from 10 countries of the world. The problem of heavy metal pollution is better known in temperate regions. Some very important studies are also published from developing countries, e.g. Hong Kong, Nigeria, Egypt, India or West-Africa. Maybe the climate has profound effect on the cycling of the elements, chemical forms, fluxes and residence times. These effects must be studied also in tropical and subtropical regions before models of global cycles would be established.

We should never forget that the environmental protection is above all for the people, for their health, for our future life-conditions, consequently the chapter on human health effects of the four elements is very essential.

This volume is especially useful for those scientists who want to have a general view of this topic. Not only biologists but chemists, geologists or medical doctors can find a lot of valuable information, the most important data on these elements. Some chapters endeavour to follow the pathways of the elements in the nature, demonstrating the atmospheric emission and deposition, the element content of natural waters and the transport from the air to the soil or to the sea. The terrestrial and the aquatic food chains are discussed as well as initial and long-term effects of the elements.

The most important value of this book is that it shows the way to the so-called blank spots on the map of our knowledge on lead, mercury, cadmium and arsenic.

Simple and clear line drawings, maps, diagrams and numerous tables help the better understanding of the text.

E. FARKAS

RODHE, H. - HERRERA, R. (eds): Acidification in tropical countries, SCOPE Vol. 36. John Wiley, Chichester, New York, 1988. p. 405

Acidification of the nature (soils, waters, vegetation, inorganic structures building materials,etc.) is a serious problem already throughout the whole world. By the increasing urbanization and industrialization, it may cause also in the developing countries (many of them laying in tropical areas) a hardly reversible process in the environment.

It is important to know the present situation before it would turn worse, and necessary to investigate how the results of European and North American environmental research can be used in these countries.

A workshop on the problem of acidification in tropical countries was held new Caracas in April 1986. The steering committee consisted of H. RODHE (chairman), P. DILLON, R. HERRERA, T. ROSSWALL, and E. SALATI.

The book contains 11 chapters, in three parts, prepared by 50 participants and contributors of 14 countries. Unusually the synthesis takes place in the Part I. It is followed by 5 chapters of the Part II: Background on acidification dealing with general topics in the tropics (atmospheric sulfur and nitrogen compounds, terrestrial and aquatic ecosystems and effects of corrosion on structures and cultural property).

Part III contains the most interesting and important chapters of the volume, the case studies of 5 countries (Venezuela, Brazil, Nigeria, China and Australia). Originally 7 case studies were planned, but unfortunately case studies of Bangladesh and India could not be completed and published.

Case studies help to answer the question: what kind of research and training programs would be helpful in increasing our knowledge about the biogeochemical cycles of sulfur and nitrogen in the tropics, including the effects caused by human induced perturbations on these cycles?

Authors apply the word 'acidification' to any changes in the natural biogeochemical cycles of both acid and alkalic substances. They are dealing with also secondary effects (e.g., ozone formation caused by emission of nitrogen oxides and volatile hydrocarbons).

The words 'topics' and 'tropical' are also used in a broad sense, including the latitude belt between 30° S and 30° N.

In this way areas mainly of tropical rainforests, savannas and arid zones, partly of warm temperate and humid climatic zones are investigated.

The volume is nicely prepared, the chapters are carefully and clearly edited, well figured, tables added often can be used well in comparisons. Our knowledge (though it is limited yet) is well-summarized in this book. It should be welcomed by biologists, geologists, engineers, economists, any theoretical and empirical experts as well.

E. FARKAS

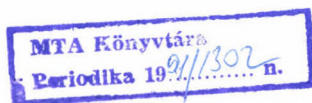
MOORE, J.W.: The Changing Environment. Springer-Verlag, New York, Berlin, Heidelberg, London, Paris, Tokyo, 1986. p. 239

The book has appeared as the 12th volume of the Springer Series on Environmental Management. Its main purpose is to review major environmental issues in the developed countries.

In order to keep these issues in perspective, conditions in developing countries are also reviewed but in less depth. After the first chapter of introduction, the second chapter devotes few pages to each of the main environmental problems in the Third World Countries, like population management and food supply, desertification, deforestation, extiction of species and toxic chemicals.

Famines became more serious after the oil price hike (1973), when the costs of agricultural commodities increased and weak economic policies resulted in a global recession. Since 1973, growth in world grain production has declined, averaging about 2 per cent per year.

Desertification, deforestation, population growth and other culturally induced environmental changes jointly made plant and animal species extinct. According to MYERS, the worldwide rate of extinction was approximately 1 species per day in 1986, is supposed to at least double by 1990, and by 2000, up to 20 per cent of all extent species will have disappeared.

While arguing for nature protection, the author follows a rather human centerd view. He takes the example of the Minke whale (Balaenoptera acutorostrata), which was considered too small to harvest but now is the most important species in the whaling industry since its bigger relatives have become so rare. His opinion is that the Minke whale should be protected till the extent of ensuring long-term meat supply. It is sad that the view of the so-called

deep ecology, which respects the existential value of living beings as well, is not mentioned in this book.

The third chapter gives useful bits of information on environmental legislation and management in the USA, Canada, UK, BDR and some other Western-European countries, Japan, the Soviet Union, some East-European countries and China. The most highly evolved state of environmental protection probably exists in the United States. The contribution of the private sector investments to it is also very high there, probably the second highest after Japan.

The author reports that "those who have travelled through the industrial regions of the Soviet Union, Eastern Europe, and China report that these has been only moderate success in controlling pollution problems". "Environmental conditions in the industrialized parts of Eastern Europe are generally poorer than those found in the Soviet Union. In Czechoslovakia and the German Democratic Republic, total budget on environmental protectionis only about 0.3 per cent of the GNP compared to 2.8 per cent for the Federal Republic of Germany." One reason for this is that "democratic nations generally respond more to public pressure than non-democratic countries."

This very interesting and informative chapter also involves some data on job loss and creation due to environmental regulations and some consideration of public attitude and awareness.

The rest of the book addresses major environmental issues: hazardous waste, groundwater contamination, toxic substances in water, toxic particulates in air, new fossil fuel technologies, nuclear energy, and acid deposition. The author discusses the generation, spread and impact of each type of pollution, and describes their health effects in detail. The pollution processes are made more clear with the help of 40 figures.

This thorough, up-to-date work can be recommended to environmental activists, teachers working in environmental education, engineers and technicians working in this field, and last but not at least, to ecologists.

J. NAGY

VENKATACHALA, B.S. - MAHESHWARY, H.K. (eds): Concepts, Limits and Extension of the Indian Gondwana. The Paleobotanist. Vol. 36. 1987. p. 378

This special volume contains the material of a five day workshop, which took place in Lucknow and was organized by the Birbal Sahni Institute of Paleobotany. It contains 42 papers and a prologe, which was written by B.S. VENKATACHALA and HARI K. MAHESHWARI.

The papers deal with the problems of the Indian Gondwana and especially with the geological and paleontological questions of the territory. The inaugural address: "Concepts, limits and extension of the Indian Gondwana" was given by D.P. DHOUNDIAL, the director general of the Geological Survey of India and skeched out th eproblems of the Indian Gondwana.

The same questions were discussed by B.S. VENKATACHALA, director of the Birbal Sahni Institute in greater details.

The following paper was written by F. AHMED, and titled, "The facts and fictions of the Gondwana concept." Its most important subject is the polar migrations and their consequences to Gondwana.

The following papers deal with the development of the Gondwana from the Early Permian till the Early Cretaceous age: B.S. VENKATACHALA and R.S. TIWARI have written about the Lower Gondwana marine incrusions periods. This is an important question, because the Gondwana idea was connected with terrestrial and freshwater sediments. S. CHAUDHURI's paper about the marine influence of Hutar Coalfield (Bihar) connects to the theme. The results are given by forams and coccolits. MANJU BANERJEE has found both litho- and bio-characteristic units in the Karharbari sediments.

The next papers deal with the boundary of Permian-Triassic.They discuss in detail the lithological, tectonical phenomen, the micro- and macrofloral elements, the types of the vegetation and the vegetation zones, the paleoclimatological data for conclusive proof of the

boundary questions. The authors are: B.C. PANDA, S.C. SHAH, S.M. CASSHYAP, R.C. REARI, A. BHUTTACHARYA, S. and A. CHANDRA, R.S. TIWARI, A. TRIPATHI, HARI K. MAHESHWARI and R. TEWARI.

The paper of D.D. PLANT tells about the origin, rise and decline of Glosspteris Flora, with notes on its paleogeographical northern boundary and age. D.C. BHRARADWAY's article deals with the palinological correlation of the Lower Gondwana coal seems.

The authors of the next two papers are SURESH C. SRIVASTAVA, NEERJA YHA and RAM-AWATAR. They have written about two Grabens palynoassemblages, which help to range the material Early Permian or Early Triassic age. A.K. SRIVASTAVA has written about the Lower Barakat flora of Raniganj Coalfield and its insect plant relationships.

S.C. GOSH, ASHIM DATTA, A. NANDI and S. MUKHOPADHYAY inform us on the Esheroid zonation in the Gondwana, lighting the Triassic connections of the subcontinent.

On the base of mega- and microfossils, stratigraphical correlation of Traissic beds has been given by SHYAM C. SRIVASTAVA and SUKH DEV.

In the next paper, H.P. SINGH and B.S. VENKATACHALA proposed the changing of the original terrestrial Gondwana concept on the base of the Upper Jurassic - Lower Cretaceous spore-pollen assemblages in the peninsular India. The case is that they have found paralic and marine sediments in many places.

The paper of HARI K. MAHESHWARI and B.N. JANA deals with the palinozonation of the Kutch Basin. The topic of the palinological research of B.S. VENKATACHALA and A. RAJANIKANTH is the age of the "Late Gondwana" floras.

Three papers were wirten about some fossils: Triassic seeds (S.R. MANIK), Late Jurassic Dicksoniaceae (Culcitites Appert) leaves (YAYASRI BANERJI), and about the geographic distribution of the genus Cicadopteris during the Upper Gondwana (NEERU PANDYA).

B.D. SHARMA and R. HARSH have made a study of the amino-acids of petrified plants from the Rajmahal Hills, with the help of paper chromatography.

The "Epiphyllous fungi from the Gondwana" has been written by USHA BAJPAI and Hari K. MAHESHWARI. The stratigraphic values of vertebrate faunas has been described in three papers by T.S. KUTTY, S.L. JAIN, T. ROY CHOWDHURY, by P. YADAGIRI, B.R.J. RAO and by P.P. SATSANGI.

RAHUL GARG, KHOWAJA ATEEQUAZZAMAN and K.P. JAIN have written about the Jurassic and Lower Cretaceous dinoflagellate cysts from India.

There is a very interesting, comprehensive paper from JAI KRISHNA: "Biological evidence for better appreciation of the Indian Gondwana. Stratigraphical, paleoclimatological, lithological and biological arguments are given.

The "Vulcanism in Gondwana" by C. TRIPATHI overspans the ages from Lower Permian till Lower Cretaceous.

Two papers deal with the limits of Indian Gondwana Plate by S.K. ACHARYA and by N.D. MITRA.

H.M. KAPOOR and GOPAL SINGH have written about extra-peninsular "Gondwana" basins stratigraphy and evolution. It connects to the "permian palynofossils from the eastern Himalaya" by SURESH G. SRIVASTAVA, ANAND-PRAKASH and TRILOCHAN SINGH.

R.S. TIWARI and VIJAYA's paper is a reflection on the relationships of the Tehyan palynoflora. The changes of the palynofloras from the Early Carboniferous-Permian-Triassic and Jurassic have been pointed out.

HARI K. MAHESHWARI and USHA BAJPAI's paper deals with the northern limits of the eastern Gondwana; it gives paleobotanical evidence.

At the end of this volume there is a paper about the coal resources in the Indian Gondwana by R.V. SAVANUR and A.K. ROY.

The technical outfit of the volume is very modern. The illustrations, figures, maps, sketches and photoplates give very high standard to the papers.

The volume is very useful for every scientist inquiring about the geology, paleontology and especially the paleobotany of the Indian Gondwana.

E. NAGY

The papers generally have the following components, which should be presented in the order listed:

1. Title, name of the author(s), affiliation, dataline, abstract, keywords
2. Text, acknowledgements
3. References
4. Footnotes
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Fekete, G., Précsényi, I. 1981: Niche structure of a perennial sandy grassland. In: Stefanovits, P., Berczik, Á., Fekete, G., Seidl, M. (eds): Man and the Biosphere Programme. Survey of 10 Years Activity in Hungary. Budapest, 68–102.
Borhidi, A., Muñiz, O., Del Risco, E. 1979*a*: Clasificación fitocenologica de la vegetación de Cuba. Acta Bot. Hung. **25**: 263–301.
Jakucs, P. 1973: „Síkfőkút Projekt". Egy tölgyes ökoszisztéma környezetbiológiai kutatása a bioszféra program keretein belül. (Síkfőkút-Project. Environmental-biological research of an oakwood ecosystem within the framework of the Biosphere program). MTA Biol. Oszt. Közl. **16**: 11–25.

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